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THE EFFECTS OF TEMPERATURE AND OTHER ENVIRONMENTAL FACTORS UPON THE PHOTOPERIODIC RESPONSES OF SOME OF THE HIGHER PLANTS[1]

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INTRODUCTION

Ever since the demonstration of the principle of photoperiodism by Garner and Allard in 1920 (*1*), [2] it has been believed by some workers that there are certain plants which will blossom only in a long- or a short-day environment. That is, it is considered that photoperiod has a specific effect upon the induction of the flowering state which is possessed only by this environmental condition. This view has persisted in spite of the fact that it has been known for a considerable time that celery (*9*), beets (*10*), lettuce (*11*), and stocks (*4*), which give responses to photoperiod, have been induced to blossom by "chilling" and that soybeans do not give the expected reaction to length of day when growing at high temperatures (*3*).

It has been briefly reported that the photoperiodic responses of a number of plants are modified by temperature (*7*). Since that report was made further trials have been completed, giving a total of more than 40 species and varieties which show altered reactions to length of day when growing at different temperatures. This list includes plants which are commonly considered to be specifically photoperiodic in their reactions. The present report is a presentation of the observations upon which these preliminary statements are based.

MATERIALS

A larger variety of plants was grown than was needed to test the effect of environmental treatments upon blossoming, as it was desired to secure samples from blossoming (reproductive) and nonblossoming (vegetative) plants to use in further studies of the obvious relation between the anatomical condition of the plant and its flowering state (*12*), especially the characteristics of the phloem (*8*). The list includes representatives of more than 40 families, 80 genera, and 120 species and varieties. The families and species follow:

Gramineae: *Zea mays, Holcus sudanensis, H. sorghum, Panicum miliaceum, Phalaris arundinacea, Phleum pratense, Avena sativa, Triticum aestivum, Secale cereale, Hordeum vulgare, Poa bulbosa, P. pratensis, Agropyron repens.*
Liliaceae: *Asparagus officinalis.*
Moraceae: *Cannabis sativa.*
Urticaceae: *Urtica dioica.*
Polygonaceae: *Fagopyrum esculentum.*
Chenopodiaceae: *Chenopodium album; Beta vulgaris, Spinacia oleracea.*
Amaranthaceae: *Amaranthus retroflexus, A. graecizans.*
Aizoaceae: *Tetragonia expansa.*

[1] Received for publication August 19, 1937; issued May 1938.
[2] Reference is made by number (italic) to Literature Cited, p. 677.

Portulacaceae: *Portulaca grandiflora.*
Caryophyllaceae: *Dianthus plumarius.*
Ranunculaceae: *Delphinium cultorum.*
Capparidaceae: *Cleome spinosa.*
Cruciferae: *Thlaspi arvense, Capsella bursa-pastoris, Brassica oleracea, B. rapa, B. pekinensis, B. alba, Matthiola bicornis.*
Crassulaceae: *Bryophyllum proliferum.*
Leguminosae: *Phaseolus vulgaris, P. coccineus, Soja max, Medicago sativa, Melilotus alba, M. dentata, Trifolium repens, Baptisia australis, Mimosa pudica.*
Geraniaceae: *Pelargonium hortorum.*
Oxalidaceae: *Oxalis corniculata.*
Tropaeolaceae: *Tropaeolum majus.*
Euphorbiaceae: *Euphorbia pulcherrima, Ricinus communis.*
Balsaminaceae: *Impatiens balsamina.*
Malvaceae: *Althaea rosea, Gossypium hirsutum.*
Violaceae: *Viola tricolor.*
Begoniaceae: *Begonia semperflorens.*
Onagraceae: *Clarkia elegans, Oenothera pratensis, Fuchsia hybrida.*
Umbelliferae: *Daucus carota, Petroselinum hortense, Apium graveolens.*
Plumbaginaceae: *Plumbago capensis, P. indica.*
Apocynaceae: *Vinca minor.*
Asclepiadaceae: *Asclepias syriaca.*
Convolvulaceae: *Ipomoea purpurea, I. batatas.*
Polemoniaceae: *Phlox paniculata.*
Verbenaceae: *Verbena hybrida.*
Labiatae: *Salvia splendens.*
Solanaceae: *Solanum tuberosum, S. pseudocapsicum, Nicotiana affinis, N. sanderae N. tabacum, Datura stramonium, Petunia hybrida, Salpiglossis sinuata.*
Scrophulariaceae: *Antirrhinum majus.*
Plantaginaceae: *Plantago major.*
Acanthaceae: *Beloperone guttata.*
Cucurbitaceae: *Cucumis sativus, Luffa cylindrica.*
Compositae: *Cichorium intybus; Lactuca sativa; Chrysanthemum morifolium; C. maximum; Anthemis cotula; Rudbeckia laciniata; Helianthus maximiliani; Cosmos bipinnatus; C. sulphureus; Aster novae-angliae; Tagetes erecta; Gaillardia amblyodon; Cirsium arvense; Solidago canadensis; Sonchus oleraceus.*

More than one variety of a single species was grown in the following cases: Four corn, two timothy, three oats, two wheat, two rye, two barley, two sugar beet, two turnip, four soybean, two morning-glory, two potato, two tobacco, two cucumber, and two orange cosmos.

A minimum of four plants of each variety was used as a unit, for each treatment employed. Larger numbers were commonly grown. The tests of the more important species were repeated two to four times.

METHODS

Duplicate sets of plants were grown in two greenhouses during the winter of 1936–37, one house being carried at a minimum (night temperature) of 70° F. and the other at 55°. These temperature treatments will be referred to as the "warm" and "cool" environments. There was little variation from these temperatures during the daytime until late spring. After April 1 the cool house would sometimes be warmer during the daytime but to no great extent until after May 1, owing to the marked absence of high temperatures in early 1937. Outdoor maximum temperatures exceeded 60° on only 4 days until May 1 and 70° only twice before May 21. Minimum temperatures were above 55° on only 2 days prior to May 29. Plants from the cool house were transferred to out-of-door temperatures a little after danger from frost was judged to be passed, May 26.

A limited series of plants was grown during the winter season at an intermediate temperature of about 63° F.

Half of each lot of plants in the warm house and in the cool house was placed in a long-day and half in a short-day environment. The long-day condition was provided by ordinary electric lights, burning from before sunset until midnight. These delivered from 30 to 80 foot-candles, as measured by a Weston photometer, to the place where the plants were situated. Their use was discontinued May 28. The short-day treatment was the normal winter day from October 15 until March 1. Beginning on that date the light exposure was artificially shortened to approximately 9 hours.

Except as otherwise noted, the plants were grown in soil and watered according to greenhouse practice.

Other environmental treatments which were employed on a smaller number of varieties were bank-sand culture (low nitrogen), partial defoliation (fig. 1), shading (light intensities of 10 to 15 foot-candles), girdling, and chilling. Many plants were shifted from one environment to another at different stages in their development and others were grown with different branches or parts of the plant in the long- and short-day environments.

OBSERVATIONS

TEMPERATURE AND PHOTOPERIOD

The time factor should be carefully considered when determining the photoperiod classification of a plant. An inspection of the literature on photoperiodism shows a general tendency to call a plant a long- or a short-day one if blossoming is merely hastened by added light or by a shortened daily light exposure. In the present trials, in which different temperatures were employed, the time required to flower was largely ignored and the periodism of a plant was determined by whether the reproductive characteristics were readily induced by a treatment, even though actual blossoming was at a considerably later time (fig. 2).

Among the more than 40 species and commercial varieties of plants that give unlike responses to length-of-day environments when grown in different temperatures, there are a number which are of special interest. For instance, poinsettia, which is habitually considered to be a short-day plant, failed to blossom in short days when grown at a minimum temperature of 70° F. from September until April (fig. 3). On the other hand, 60 percent of the 20 plants which were given a long-day treatment blossomed at a temperature of 55°. Plants in an intermediate temperature of 63° to 65° gave the anticipated response of short-day blossoming and long-day vegetative growth.

This influence of temperature upon photoperiodism is not confined to short-day plants, as is demonstrated by the results with *Rudbeckia laciniata*. This long-day plant has consistently remained a rosette and failed to produce stems in previous short-day experiments (temperatures of 60° to 65° F.) (*6*). On the other hand, when grown at 55° it not only produced stems, but these formed blossom buds in the short-day treatment, after a relatively long time—a definite refutation of the commonly reported habits of this plant (figs. 4 to 7). The long-day cool plants produced abnormal blossoms (fig. 5), but with

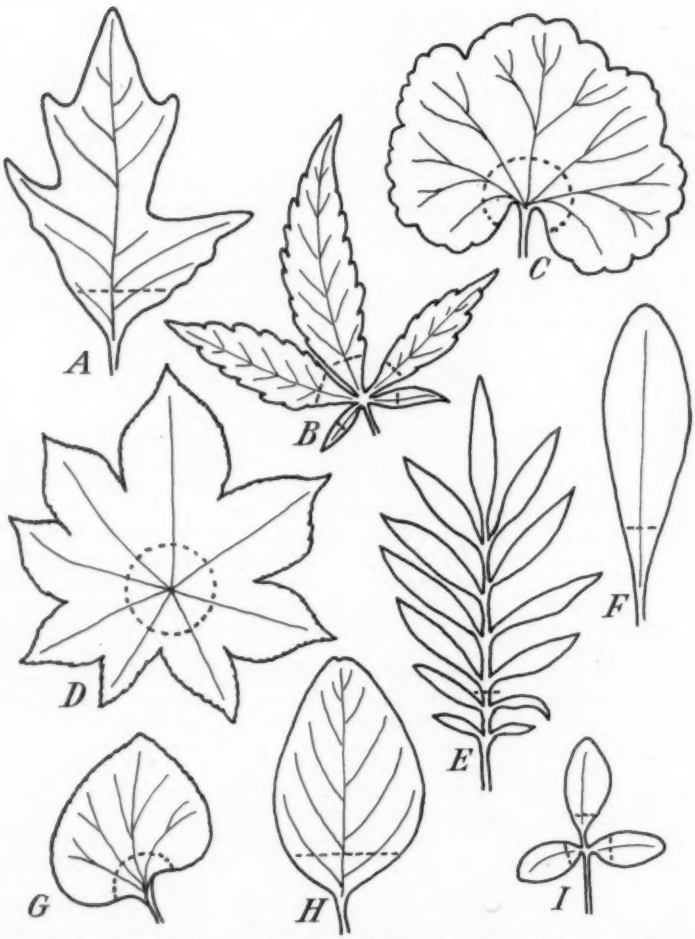

FIGURE 1.—Diagram of leaf outlines to illustrate the "defoliation" method (dotted lines): *A*, Poinsettia; *B*, hemp; *C*, geranium; *D*, castor-bean; *E*, marigold; *F*, stock; *G*, begonia; *H*, pigweed; *I*, sweetclover.

warmer temperatures became more like the usual type. The sow-thistle also remained as a rosette, in the short-day warm house, but produced a typical stem and fruited in the short-day cool house.

FIGURE 2.—Fuchsia blossomed in all environments but after different lengths of time. Such a variety should be classified as indeterminate and not as long-day: *A*, Cool, short-day; *B*, cool, long-day; *C*, warm, short-day; *D*, warm, long-day.

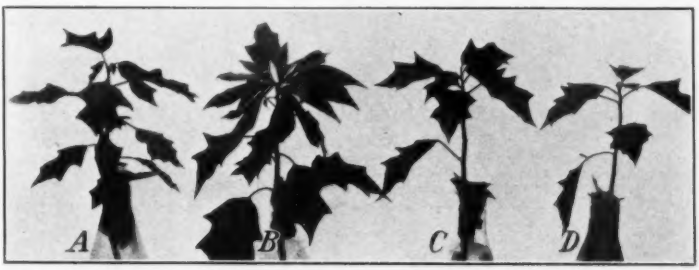

FIGURE 3.—Tips of poinsettia plants grown in different temperatures, all in short days: *A*, 70° F. minimum (vegetative); *B*, 63° (flowering); *C*, 55° (vegetative, slowly) *D*, changed from 65° to 70° (flowers abscissed).

Klondike cosmos (a "specifically short-day plant") did not blossom in the short-day warm house. In the cold treatments it grew very slowly, the long-day plants showing as much tendency to blossom as did the short-day plants (figs. 8 and 9).

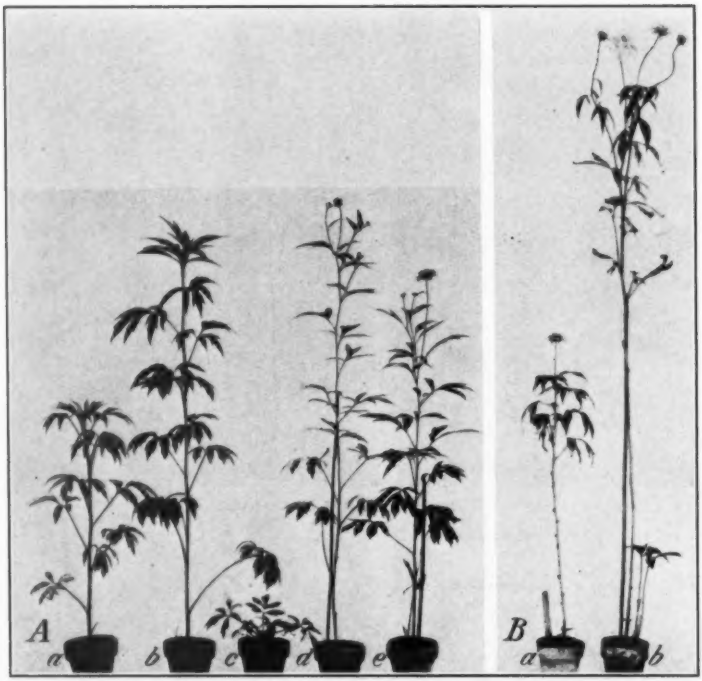

FIGURE 4.—Temperature affects blossoming of rudbeckia: *A*, Photographed February 8; *a*, cool, short-day; *b*, cool, long-day; *c*, warm, short-day; *d*, warm, long-day; *e*, changed warm, long-day to warm, short-day. *B*, Photographed April 15; *a*, cool, short-day; *b*, cool, long-day. The production of shoots in cool, short days (*A*, *a*) is in striking contrast to the rosettes (*A*, *c*) in warm, short days (*6*). This same condition occurs with sow-thistle and with chicory (fig. 25).

FIGURE 5.—*Rudbeckia* blossoms: *A*, Warm, long-day to cool, long-day; *B*, cool, long-day; *C*, cool, long-day to warm, long-day; *D*, warm, long-day.

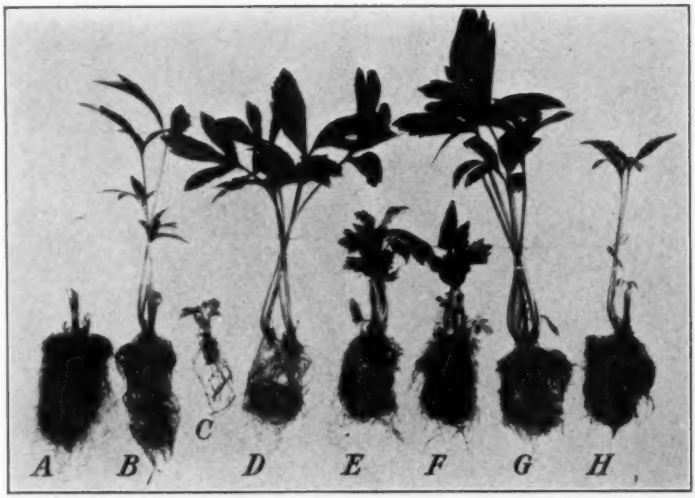

FIGURE 6.—Root production and new foliage regeneration of rudbeckia, photographed April 15: *A*, Cool, short-day; *B*, cool, long-day; *C*, warm, short-day (original foliage); *D*, warm, long-day; *E*, warm, long-day to warm, short-day; *F*, cool, short-day to warm, short-day; *G*, cool, long-day to warm, long-day; *H*, warm, long-day to cool, long-day. Note the greater root system of *A* than *B*. *A* is a small plant (fig. 4, *B*, *a*) and *B* is a large plant (fig. 4, *B*, *b*). *B* blossomed earlier than *A*.

FIGURE 7.—Effect of previous culture upon regeneration of rudbeckia, photographed June 28. Plants under common culture since April 15. Environments of previous culture period as shown in legend of figure 6. The warm, short-day plants died (*C*). Plants with a previous warm, long-day treatment did not produce flower stems.

FIGURE 8.—Klondike cosmos, photographed March 22: *A*, Cool, short-day; *B*, cool, long-day; *C*, medium-temperature, normal-day (the only fruiting plants); *D*, warm, short-day (just beginning to elongate preceding blossoming, since the day was shortened to 9 hours March 1); *E*, warm, long-day.

The horticultural variety of Klondike cosmos, Orange Flare, which blossoms in midsummer, gave a most interesting response. It was assumed that this variant of the short-day Klondike was a long-day type. The results of the environmental treatments proved otherwise. In the cool-temperature environment it did give a short-day response, but in the warm house it blossomed under both the short- and long-day treatments (fig. 10). Very obviously, therefore, this variety blossoms in the summertime out of doors because of high temperatures and not because of long days.

Probably the most interesting plant from a historical viewpoint is Maryland Mammoth tobacco, for it was from the short-day reactions of this variety that the photoperiodism concept originated (*1*). To

FIGURE 9.—Young plants of Klondike cosmos. Only the intermediate-temperature plants blossomed *A*, Cool, short-day; *B*, cool, long-day; *C*, intermediate-temperature normal-day; *D*, warm, short-day *E*, warm, long-day.

those who would be inclined to look upon photoperiod as having a specific effect in inducing reproduction, in contrast to the view that blossom-bud formation depends upon the internal condition of the plant (*5*), this tobacco would naturally be a key plant by which to test the specific nature of photoperiodism. Seedling plants started in long-day warm conditions in September were still vegetative in May. Plants which were old enough to have several leaves, became reproductive in only 3 or 4 weeks after being transferred to the short-day, warm environment. The rate of growth was slower in the short-day, cool location, but blossom buds were soon formed. The plants in the long-day cool location took on the growth habits of reproductive plants within a few weeks after being transferred, and clearly formed blossom buds after 2½ to 3 months' exposure (fig. 11). That is, Maryland Mammoth tobacco became reproductive in long days when growing at a cool temperature.

FIGURE 10.—Orange Flare cosmos, a summer-blossoming variant of Klondike: *A*, Cool, short-day; *B*, cool long-day; *C*, warm, short-day; *D*, warm, long-day. The long-day blossoming of this variety illustrates a temperature "sport."

FIGURE 11.—Maryland Mammoth tobacco: *A*, Photographed April 19, treatments begun January 15 *a*, Cool, short-day; *b*, cool, long-day (budding); *c*, warm, short-day (fruited and regenerating;) *d*, warm long-day. *B*, Photographed May 26: *a*, Cool, long-day (budding); *b*, warm, long-day.

Some other responses of particular interest follow: The tobacco variety Havana No. 38 (fig. 12) blossomed first in long days in the warm temperature, but in all environments after different lengths of time. Other plants giving a similar reaction were buckwheat,

FIGURE 12.—Havana No. 38 tobacco blossomed first in long days but eventually in all environments: *A*, Cool, short-day; *B*, cool, long-day; *C*, warm, short-day; *D*, warm, long-day.

fuchsia (fig. 2), mustard (white), nasturtium (fig. 13), New Zealand spinach, and pepper. Morning-glory (var. Heavenly Blue) blossomed in short-day warm and long-day cool locations (fig. 14). When the day length was shortened from the normal winter day of March to 9 hours, cosmos and poinsettia plants which had remained vegetative all winter in the warm house became reproductive.

FIGURE 13.—Nasturtium budded and flowered in all environments but after different lengths of time: *A*, Cool, short-day; *B*, cool, long-day; *C*, warm, short-day; *D*, warm, long-day.

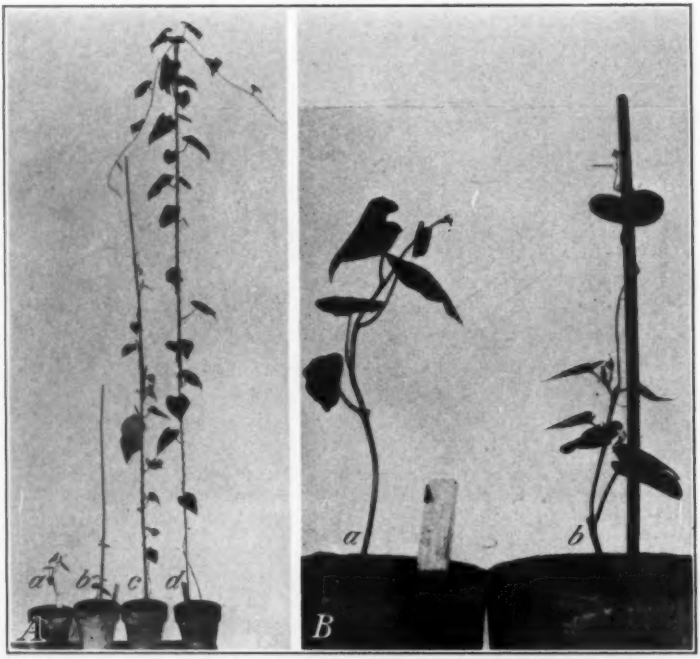

FIGURE 14.—Morning-glory (Heavenly Blue) blossomed in warm, short-day and cool, long-day environments: *A*: *a*, Cool, short-day; *b*, cool, long-day; *c*, warm, short-day; *d*, warm, long-day. *B*: Close-up of cool short-day (*a*) and cool, long-day (*b*) plants.

Some plants blossomed in only one of the environmental combinations, for example, bluegrass (short-day cool) (fig. 15), chrysanthemum var. Lillian Doty (short-day warm) (fig. 16), Cleome (long-day warm) (fig. 17), white clover (long-day cool) (fig. 18), and salvia (short-day cool). Others blossomed in one temperature with relatively little regard to length of day. Examples of these were German stocks (cool) (fig. 19), field corn (warm) (fig. 20), bush bean (warm), pansy (cool), phlox (warm) (fig. 21), and geranium (cool) (fig. 22). A few plants gave similar photoperiodic reactions in both the warm and cool environments. These were spring oats (var. Victory) (fig. 23), winter oats (fig. 24), spring barley (Oderbrucker), chicory (fig. 25), lambsquarters, fall aster, Shasta daisy, dogfennel (fig. 26), annual sugar beet (fig. 27), and possibly *Melilotus dentata* (fig. 28).

No blossoms were produced on such species as potato (figs. 29, 30), sweetpotato, and variegated geranium in any of the environments provided.

Canada thistle, plantain, and wild sunflower plants made no appreciable growth throughout the winter in any of the four environments. Plants of these species collected after the ground had thawed in April grew readily, suggesting that a period of chilling had broken their "rest period."

The species and varieties which gave different photoperiod responses at different temperatures during the winter and spring of 1936–37 were: Alfalfa (seed setting), winter barley, castor-beans, bush beans, beets (fig. 31), bulbous bluegrass, Kentucky bluegrass, bryophyllum (fig. 32), Chinese cabbage, reed canary grass (fig. 33), celery, chrysanthemum var. Lillian Doty, Cleome, white clover, corn var. Golden Glow, Klondike cosmos, Orange Flare cosmos, cucumber, geranium, gourd, hemp, jimsonweed (fig. 34), lettuce (fig. 35), morning-glory, pansy, pigweed, phlox, plumbago, poinsettia, quackgrass (fig. 36), rudbeckia, spring rye, winter rye, salvia, soybean var. Illini (fig. 37), squash, stock, Sudan grass, sowthistle, timothy (figs. 38, 39), Maryland Mammoth tobacco, tumbleweed (fig. 40), spring wheat, and winter wheat (fig. 41).

The unlike responses of different branches or parts of a plant when these are given different photoperiod environments constitute one of the interesting angles of the phenomenon of photoperiodism (*2*, *6*). This customary result was not secured when morning-glory plants were placed with part of the plant exposed to one photoperiod treatment and the remainder to another. At warm temperature the variety Heavenly Blue behaved as a short-day plant. Plants with the bases (2 feet) and lower branches in a short-day environment and the tops in a long-day blossomed throughout. Plants with the bases in a long-day environment and the tops in a short-day gave a delayed response but also blossomed in both environments. Plants in a long-day environment did not blossom (fig. 42). Unlike some other species, the morning-glory appears to respond systemically and not locally. Also the reproductive state may originate in the base as well as in the upper portion.

In the case of plants which were unfavorably affected in their growth and fruiting responses by the warm environment, added light (long-day treatment) frequently aggravated the temperature injury instead of being a compensating factor (figs. 15, 31, 33).

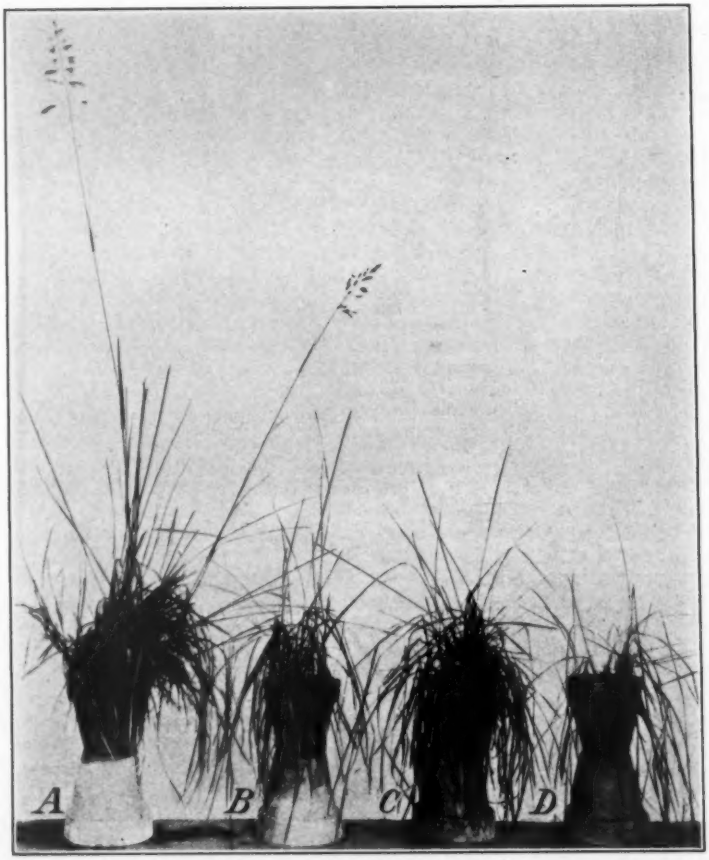

FIGURE 15.—Kentucky bluegrass: *A*, Cool, short-day; *B*, cool, long-day; *C*, warm, short-day; *D*, warm, long-day.

FIGURE 16.—Chrysanthemum var. Lillian Doty: *A*, Cool, short-day; *B*, warm, short-day; *C*, cool, long-day *D*, warm, long-day. Plants that are kept cool sucker instead of producing stems. These plants were practically the size shown when the treatments began.

FIGURE 17.—Cleome thrives only in long days and at warm temperature: *A*, Cool, short-day; *B*, cool long-day; *C*, warm, short-day; *D*, warm, long-day.

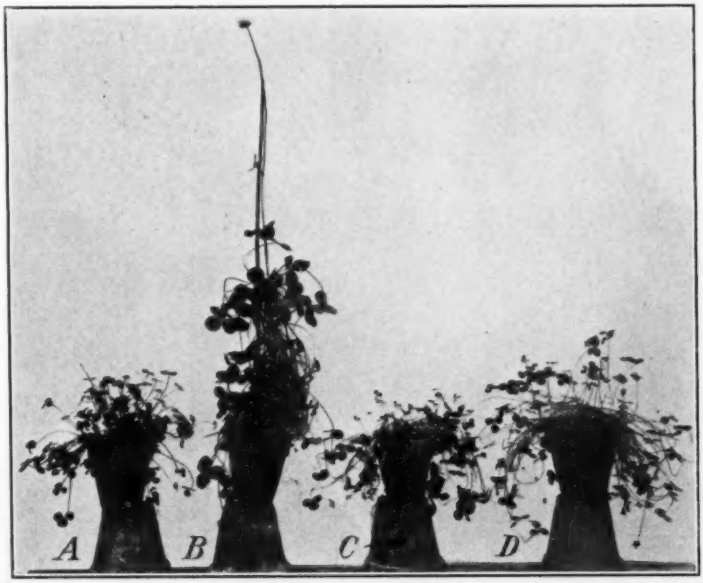

FIGURE 18.—White clover becomes a "giant" plant in a cool, long-day environment: *A*, Cool, short-day; *B*, cool, long-day; *C*, warm, short-day; *D*, warm, long-day.

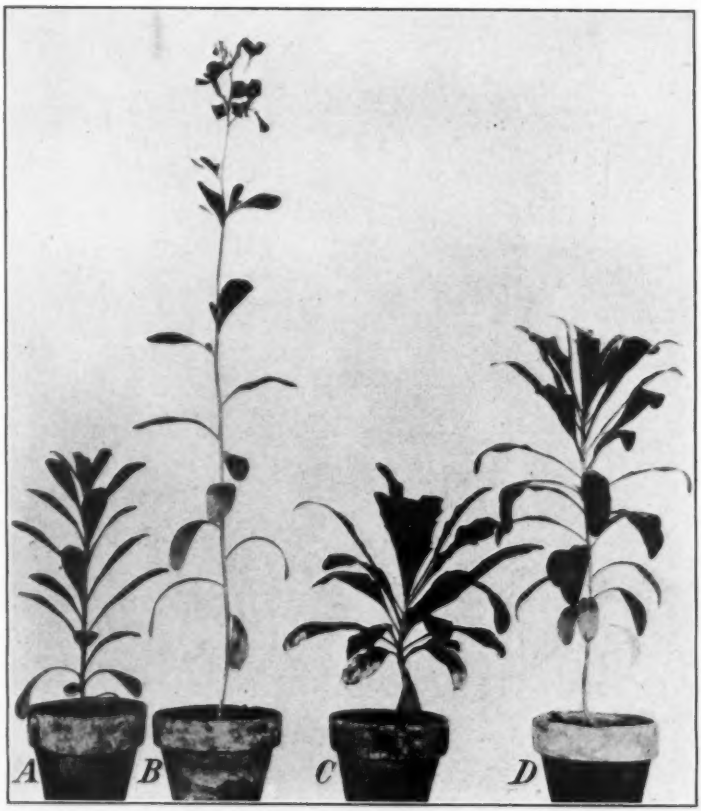

FIGURE 19.—Stocks blossom only at cool temperatures: *A*, Cool, short-day (budding); *B*, cool, long-day *C*, warm, short-day; *D*, warm, long-day.

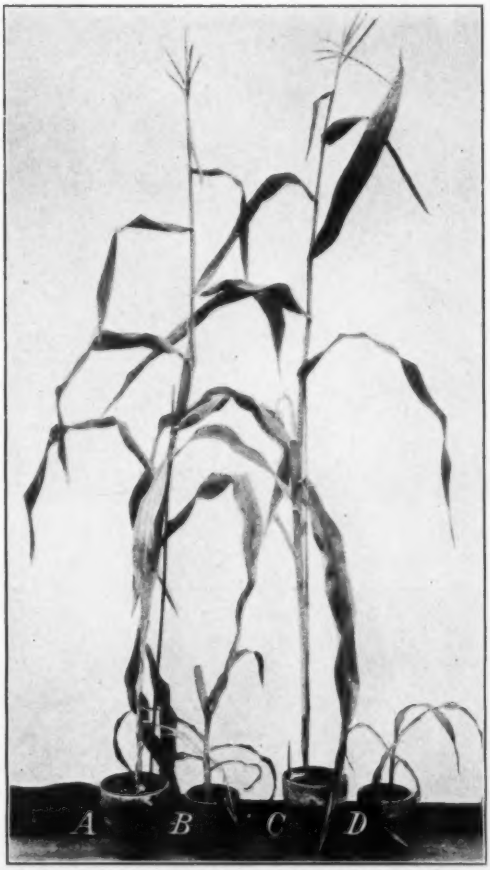

FIGURE 20.—Corn (Golden Glow) is insensitive to photoperiod at high temperatures, although it responds at intermediate temperatures (6): *A*, Warm, short-day; *B*, cool, short-day; *C*, warm, long-day; *D*, cool, long-day.

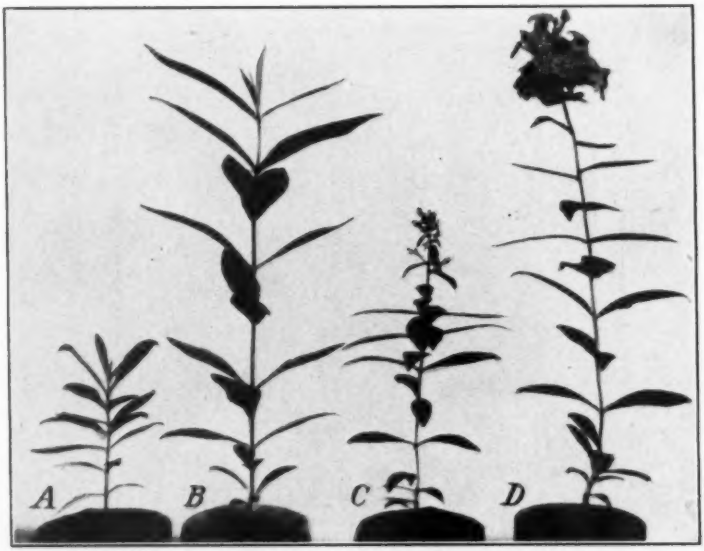

FIGURE 21.—Phlox blossoms at warm temperatures: *A*, Cool, short-day; *B*, cool, long-day; *C*, warm, short-day; *D*, warm, long-day.

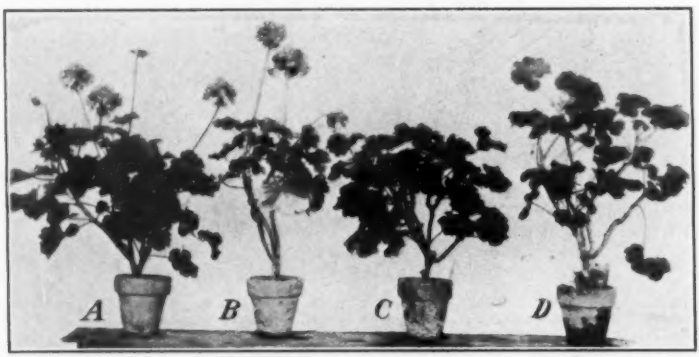

FIGURE 22.—Geranium blossomed better in a cool temperature: *A*, Cool, short-day; *B*, cool, long-day *C*, warm, short-day; *D*, warm, long-day.

FIGURE 23.—Victory oats: *A:* *a*, Cool, short-day; *b*, cool, long-day; *c*, warm, short-day; *d*, warm, long-day. *B:* Roots of plants in *A*. Fruiting plants had less roots; early fruiting (*d*) had much less than if a good leaf development had preceded heading (*b*). Compare with figure 41.

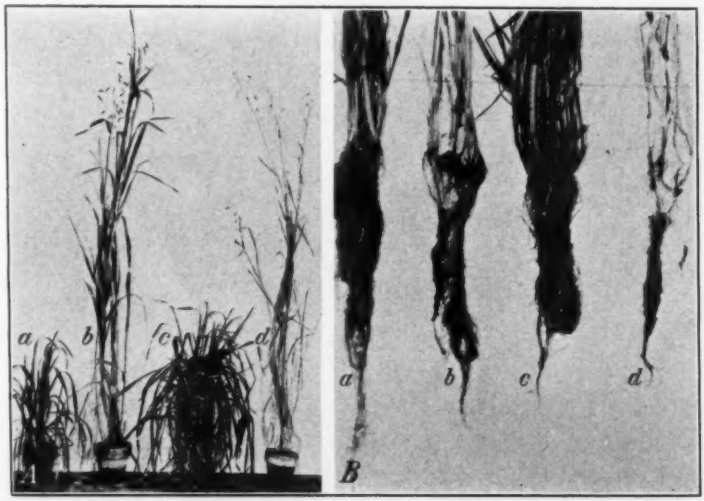

FIGURE 24.—Winter oats shows more adaptation to temperature than Victory (fig. 23). With more foliage it also shows more rooting; same arrangement of plants and lettering as in figure 23.

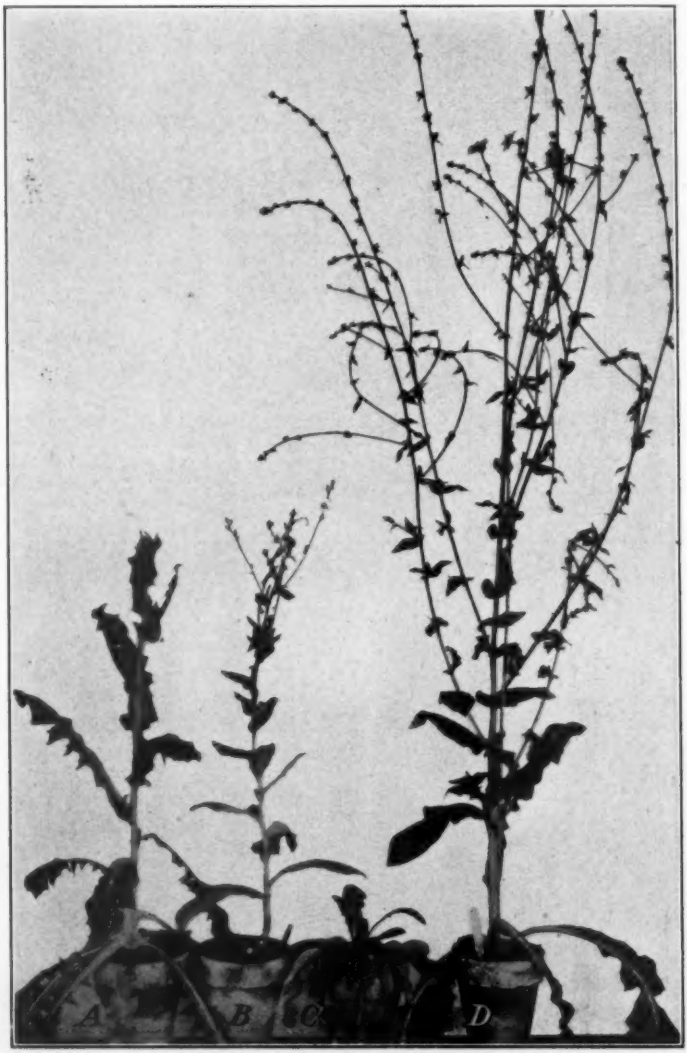

FIGURE 25.—Chicory fails to produce shoots under warm, short-day treatment: *A*, Cool, short-day (budding); *B*, cool, long-day; *C*, warm, short-day; *D*, warm, long-day.

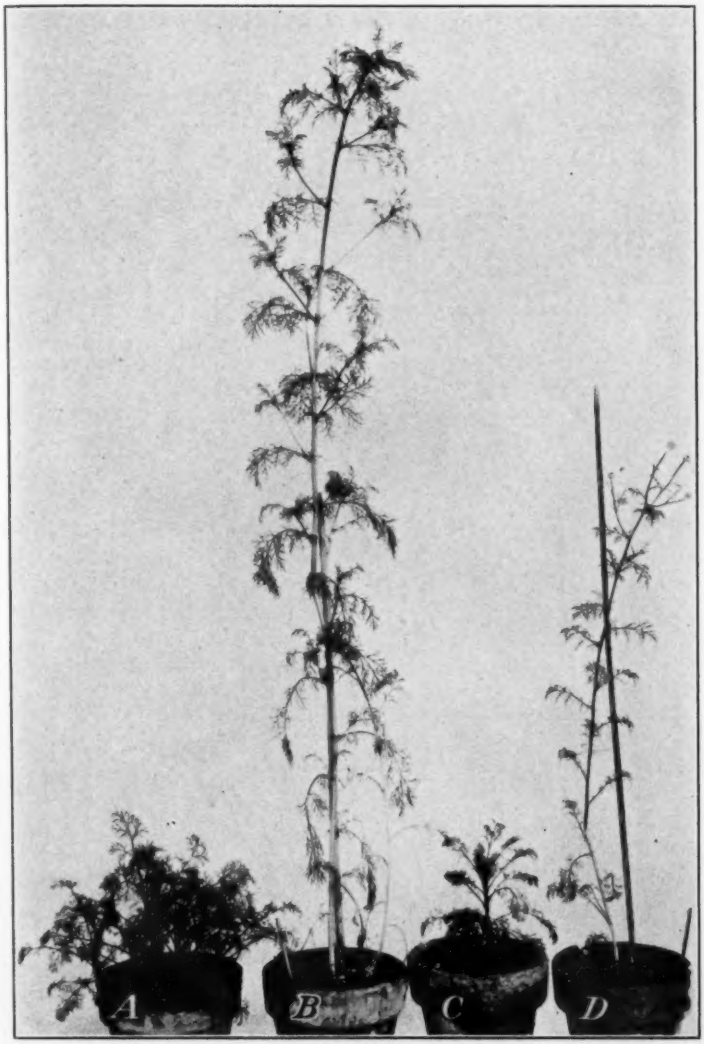

FIGURE 26.—Dogfennel blossoms about equally at different temperatures: *A*, Cool, short-day; *B*, cool long-day; *C*, warm, short-day; *D*, warm, long-day.

FIGURE 27.—Annual sugar beets (No. 2240) need long days to produce first-season "bolting": *A*, Cool, short-day; *B*, cool, long-day; *C*, warm, short-day; *D*, warm, long-day. Compare with figure 31.

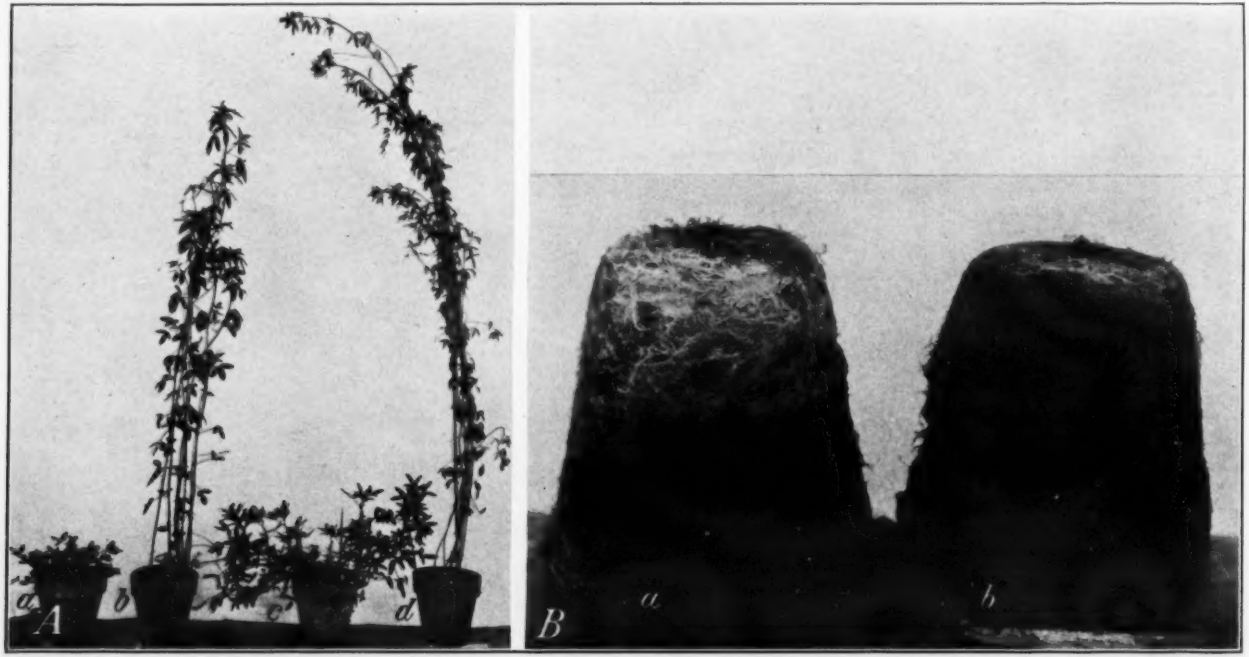

FIGURE 28.—Siberian sweetclover (*Melilotus dentata*), 8-weeks treatment: *A:* *a*, Cool, short-day; (*b*), cool, long-day (budding); *c*, warm, short-day; *d*, warm, long-day (blossoming). *B:* Soil from pots of warm, short-day (*a*) and warm, long-day (*b*) plants showing root differences. The tall, fruitful plant has fewer roots.

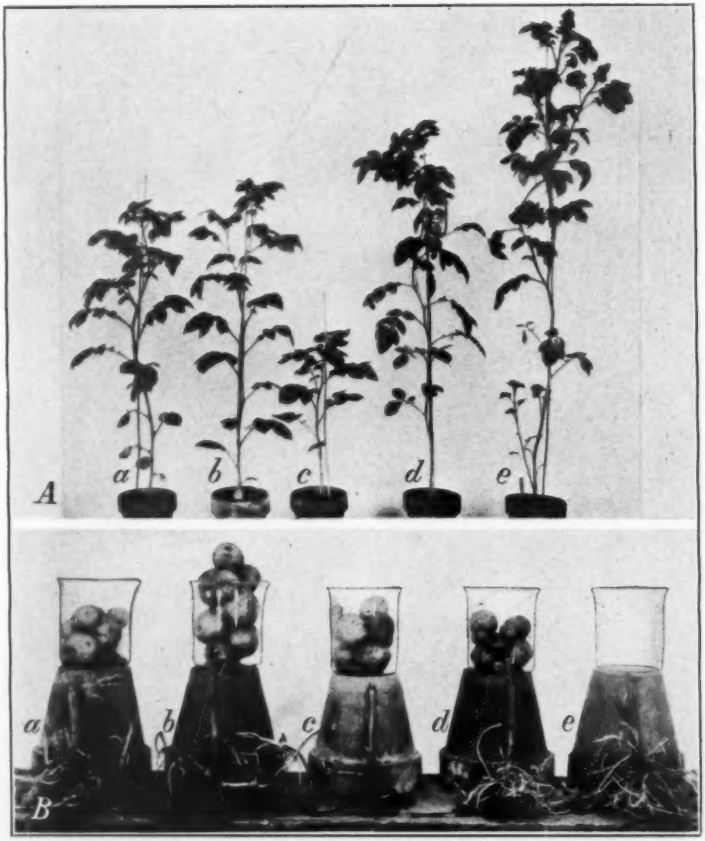

FIGURE 29.—Triumph potato, photographed March 17: *A*, Top growth: *a*, Cool, short-day; *b*, cool, long-day; *c*, medium temperature, normal-day; *d*, warm, short-day; *e*, warm, long-day. *B*, Roots of one plant and tubers from three plants of each lot arranged and lettered as in *A*.

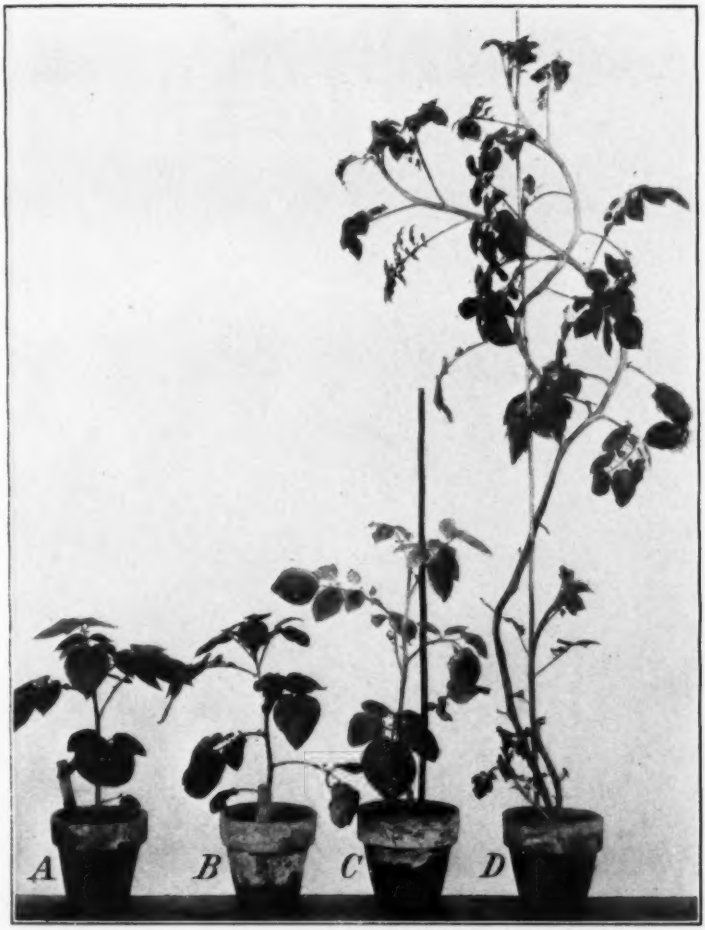

FIGURE 30.—Irish Cobbler potato grows slowly except under long-day, warm condition (compare with fig. 29, *A*): *A*, Cool, short-day; *B*, cool, warm-day; *C*, warm, short-day; *D*, warm, long-day.

FIGURE 31.—Table beet var. Early Wonder; *A*, Cool, short-day; *B*, cool, long-day; *C*, warm, short-day; *D*, warm, long-day. Compare with figure 27.

FIGURE 32.—Long-day (*B*) bryophyllum plants regenerate abundantly; short-day plants do not (*A*).

FIGURE 33.—Reed canary grass: *A*, Cool, short-day; *B*, cool, long-day; *C*, warm, short-day; *D*, warm, long-day.

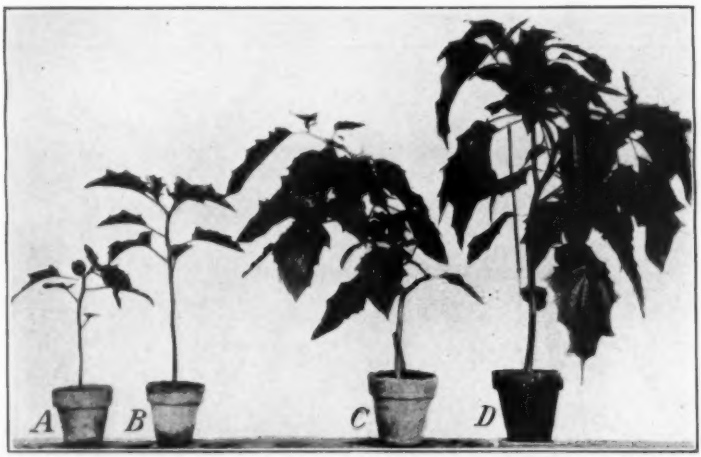

FIGURE 34.—Jimsonweed responded to temperature as well as to photoperiod: *A*, Cool, short-day (fruiting); *B*, cool, long-day (blossoming); *C*, warm, short-day (blossoming); *D*, warm, long-day (vegetative).

FIGURE 35.—Lettuce blossoming varied with temperature, nutrient, and photoperiod: *A*, Cool, short-day; *B*, cool, long-day (beginning to bolt); *C*, cool, long-day (same age as *B*) in sand culture (low nitrogen); *D*, warm, short-day; *E*, warm, long-day.

FIGURE 36.—Quackgrass: *A*: *a*, "Fruiting" habit of *Poa bulbosa*, a cool, short-day-preference plant; *b*, cool, short-day; *c*, cool, long-day (heading); *d*, warm, short-day; *e*, warm, long-day (sterile stems). *B*: Roots of quackgrass plants arranged as in *A*. Fruiting plants (*b*) are producing underground shoots.

FIGURE 37.—Soybean var. Illini. Flowering varied with temperature as well as photoperiod: *A*, Cool, short-day; *B*, cool, long-day; *C*, warm, short-day (fruiting); *D*, warm, long-day.

FIGURE 38.—Two unknown varieties of timothy (*A* and *B*), showing different responses to environment: *a*, Cool, short-day; *b*, cool, long-day; *c*, warm, short-day; *d*, warm, long-day.

FIGURE 39.—Vegetative regeneration of "sterile" stems of timothy. See figure 38, *A*, *d*.

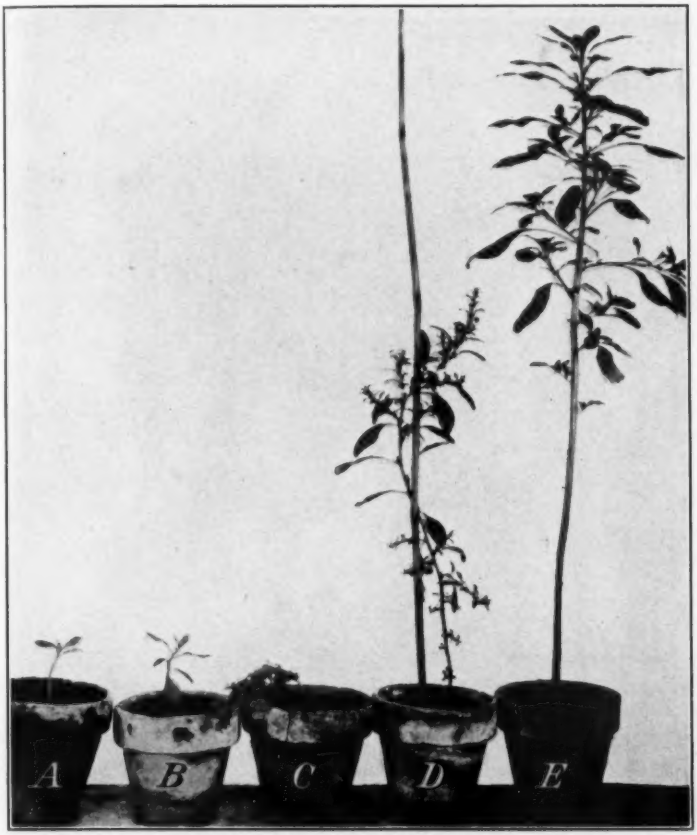

FIGURE 40.—Tumbleweed, photographed March 27: *A*, Cool, short-day; *B*, cool, long-day; *C*, medium-temperature, normal-day (fruiting); *D*, warm, short-day (fruiting); *E*, warm, long-day (vegetative).

FIGURE 41.—Winter wheat: *A*, Tops: *a*, cool, short-day; *b*, cool, long-day; *c*, warm, short-day; *d*, warm, long-day. *B*, Abundant roots follow leafy tops. Lettering in same order as *A*. Compare with figures 23 and 24.

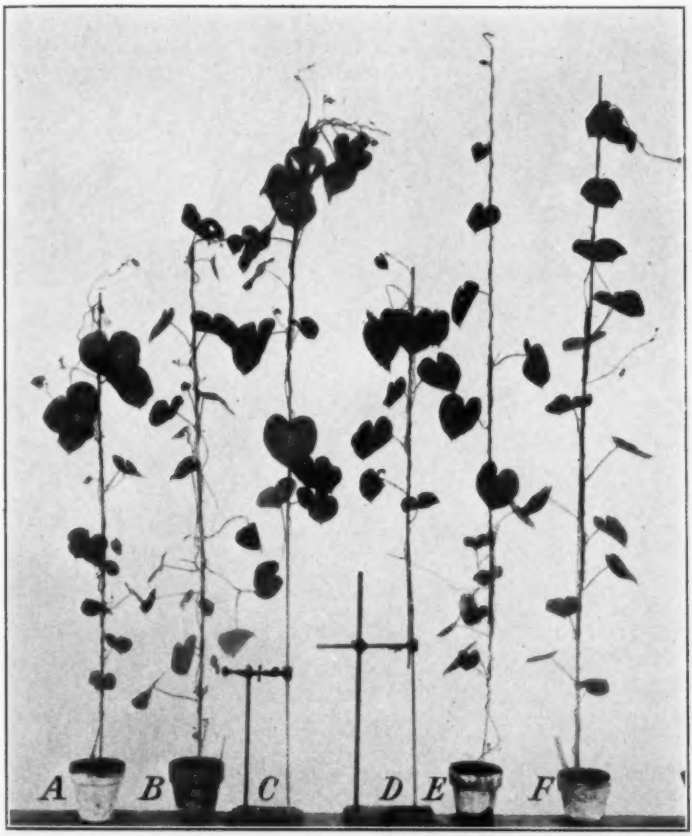

FIGURE 42.—Plants of warm-temperature morning-glory var. Heavenly Blue: *A*, Short-day (blossoming); *B*, base and branches, short-day (blossoming); *C*, top of plant *B*, long-day (blossoming); *D*, top of plant *E* short-day (budding); *E*, base and branches, long-day (budding); *F*, long-day (vegetative). Blossoming was induced by any part of the plant being under short-day treatment.

From the performance of some plants such as portulaca, dianthus, and celery (fig. 46) it appears that variable temperatures and/or light conditions would be more conducive to flowering than uniform environmental conditions.

OTHER ENVIRONMENTAL FACTORS

Other treatments than temperature were used with a few varieties of plants to affect the initiation of the reproductive state. Like temperature and photoperiod, a low nitrogen nutrient (bank-sand culture) may have opposite effects upon the time of blossoming of different plants. For example, this nutrient condition hastened the flowering of *Clarkia* but delayed it in the case of marigold (fig. 43). Previously

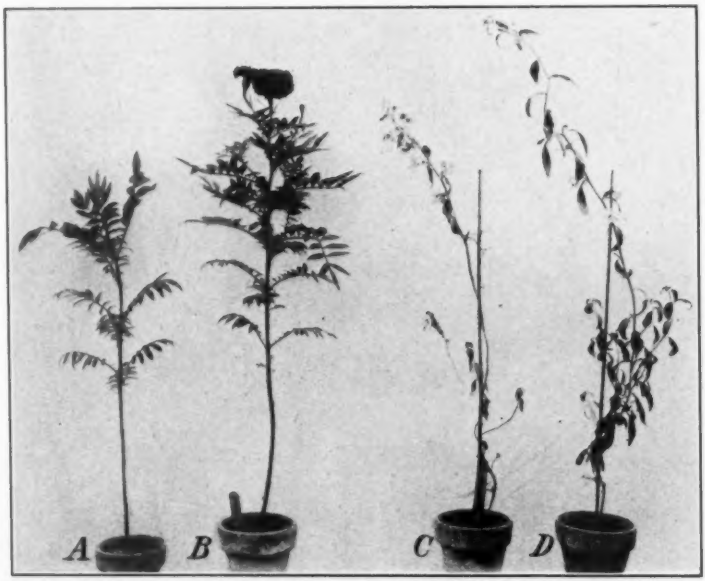

FIGURE 43.—Nutrient affects blossoming of different plants unequally: *A*, Marigold in sand (vegetative); *B*, same in soil (blossoming); *C*, Clarkia in sand (blossoming); *D*, same in soil (budding).

blossoming geranium plants which were made vegetative by a warm, short-day treatment blossomed in this environment when transferred from soil to sand.

Girdling did not induce flowering of Klondike cosmos or poinsettia. This technique is noted for giving variable results, being effective in those situations where the girdled plant is "close to becoming reproductive" (fig. 44). For instance, varieties of apples which are "early bearers" will usually make a striking response to girdling, whereas those which are known to be late bearing may show no blossom-bud formation the first season after being girdled.[3]

[3] Unpublished data.

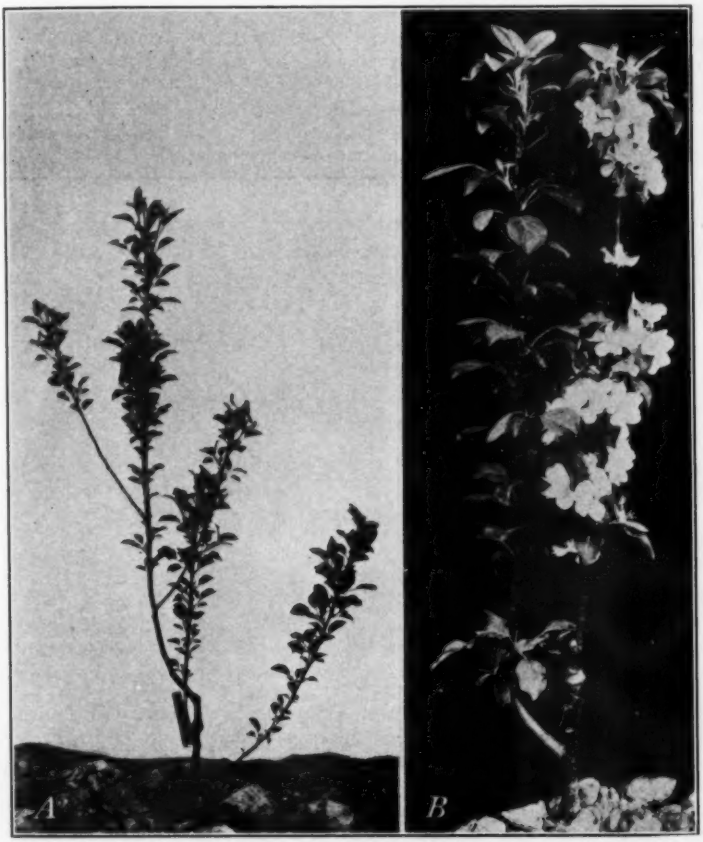

FIGURE 44.—Girdled apple trees: *A*, Winesap, still vegetative; *B*, Wealthy, blossoming. Top and suckers of Winesap much alike in foliage appearanec and bark color; Wealthy top (girdled) unlike sucker in growth characters.

Partial defoliation (fig. 1) prevents or delays blossoming (fig. 45), the degree of influence apparently being in proportion to the readiness with which the plants flower. Plants which produce blossoms at only a few of their growing points are readily inhibited from blossoming by a reduction in leaf area. On the other hand, if it is the habit of the plant to flower abundantly, defoliation has less effect upon blossom production.

Shading in which the light intensity was reduced to 10 to 15 foot-candles, had much the same type of effect as partial defoliation. It should be borne in mind, however, that the effects are different when the plants have a good soil medium than when they are grown in bank-sand culture. In the case of a low nitrogen supply, flowering may be benefited, of course, by partial shading or defoliation.

The attempt to induce bolting of celery by cool temperature was not very successful, as happened in a previous case (*6*). The following interesting result was secured with celery, however, and may explain

FIGURE 45.—Wax beans: *A*, Cool (vegetative); *B*, warm "defoliated" (vegetative); *C*, warm (fruiting).

the previous failures. While plants started in October did not produce seedstalks by May in any of the four environments, plants in the cool house but in the normal day became reproductive (fig. 46). Obviously, the shifting day length with the advent of spring had a different effect than a continuous long-day treatment. The short-day plants which had been in the cool temperature treatment began to bolt in the warm weather of June. This shows a reaction to a varying length of day at uniform temperature as well as to varying temperature with a uniform length of day.

ROOT DEVELOPMENT

The question of the root development of plants grown in different environments belongs, properly, to a later paper in which the anatomical condition of roots is to be recorded, but some of the striking relations of top and root development that have been observed should be reported without this delay.

The amount of roots the plants produce is obviously related to the extent and character of the foliage development (figs. 23, 24, 28, 29, 36, 41). The flowering state seemed to reduce root formation. Since many plants had a small amount of foliage when flowering began, these also had smaller root systems. If abundant foliage was produced prior to the advent of blossoms the fruiting plants had a more extensive root development. Root extension appears to be related to the external environment only as the latter is reflected in the character of top produced.

FIGURE 46.—"Bolting" of celery occurred under cool, natural-day rather than under short- or long-day treatment: *A*, Warm, long-day; *B*, warm, short-day; *C*, warm, normal-day; *D*, cool, long-day; *E*, cool, short-day (seedstalks beginning); *F*, cool, normal-day.

DISCUSSION

The view to be taken of the role of photoperiodism in inducing blossoming becomes altered from what it has generally been for the last 17 years when the effects of temperature upon photoperiodic responses are considered. Photoperiod is thus no longer a factor having a specific effect which cannot be much modified, but becomes, along with other external environments, one of the contributing conditions which, taken together, create an internal condition of the plant that results in blossom-bud formation (*5*). For many plants, a certain photoperiod may be a dominant requirement, but it now appears that it is not an essential one. This fact, together with the finding that the carbon dioxide exchange rhythm is correlated with the flowering state (*6*) and that the anatomical conditions of plants appear to affect blossoming (*8*, *12*), is taken as evidence that the production of blossoms may be due to a like physiological condition in many plants and not the result of a different one for each variety. While different external environments are required to induce blossoming of different varieties, the present data seem to indicate that this reaction was the result of a common type of condition within the plant.

Another item of theoretical importance is the reaction of morning-glory when growing with parts of the plant in different environments. Its systemic instead of local response would lead to the suggestion that the deduction, which has been made from some plant habits,

that photoperiod phenomena originate in the apex of the plant, should not become a generalization.

It would now appear probable that much of the uncertainty which is becoming apparent in the literature as to the proper photoperiod classification of some plants has arisen from variations in the cultural treatments other than photoperiod, such as temperature.

The influence of environment upon plant form is very apparent in many series (figs. 18, 19, 26, 28, 33, 40).

The very apparent fact that some varieties within a species show a marked adaptation to widely different environments raises this question: Is the degree of adaptation a genetic character? If it should be more definitely determined after further trials that the ability of a plant to thrive in other than a narrow range of environments is hereditary, this character should be recognized and given special consideration in the breeding and selection of agricultural varieties (figs. 23, 24, 29, 30, 38).

Since a given environment, such as photoperiod or temperature, does not have a specific effect in inducing blossoming but has a varying effect depending upon other factors, in future studies to determine why plants blossom it would seem advisable to give special attention to the internal conditions that influence blossoming. While different factors of the environment may appear at times to have a regulating effect upon the production of blossoms, it would seem that this is so only because those factors induce certain conditions within the plant which result in blossoming.

SUMMARY

The photoperiod responses of a number of plants were altered by temperatures a little above or below those usually employed in greenhouse culture. Among the plants so affected were poinsettia, Klondike cosmos, rudbeckia, soybeans, and Maryland Mammoth tobacco. The effects of other environmental treatments as well as temperature indicate that the blossoming state results directly from the nature of the internal condition of the plant rather than from any specific external treatment.

Morning-glory plants with branches in different photoperiod environments blossomed throughout instead of giving a local response as is the case with some plants such as poinsettia, cosmos, and Maryland Mammoth tobacco.

Root development was not well related to the photoperiod treatment but rather to the foliage character of the top.

Orange Flare cosmos which blossoms in the long days of summer appears to be an example of an adaptation to temperature rather than to photoperiod.

If, as appears from the responses of several varieties of plants, adaptation is a genetic character, it deserves greater consideration than is now given it in plant-breeding work.

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STUDIES ON THE PHYSIOLOGY AND INHERITANCE OF FEATHERING IN THE GROWING CHICK[1]

By M. H. RADI, *graduate student*, and D. C. WARREN, *poultry geneticist, Kansas Agricultural Experiment Station*[2]

SCOPE OF THE PROBLEM

The term "feathering" as used in this paper refers to the extent to which the bird is clothed with feathers at the time it attains the broiler stage. In a study of this type, a wide range of factors is involved since feathering is a process of growth and development subject to the effects of numerous physiological and inherent agents. A consideration of the physiological nature of feathering requires investigation of the dietary, hormonal, and environmental factors.

From the marketing standpoint, good feathering is indispensable, if a profit is to be realized, for poorly-feathered broilers are subject to severe market discrimination.

STOCK USED

The birds used in all the studies which are to be discussed were a part of the flock carried at the Kansas Agricultural Experiment Station. Approximately 3,100 birds were utilized in a period of 4 years. Three strains of the Rhode Island Red breed referred to as the early-feathering, the well-feathering, and the poor-feathering were utilized.

The early-feathering strain is characterized by early-developing and rapid-growing feathers. The rate of feathering in these birds is similar to that commonly found in the birds of the Mediterranean breeds. This type of early feathering is a heritable, sex-linked, recessive characteristic. The strain was established by selection of early-feathering chicks in a strain known not to be homozygous for the sex-linked rate-of-feathering gene.

Both the well- and the poor-feathering stocks are known to be homozygous for the sex-linked dominant allel of early feathering. These two strains were the result of plus and minus selection for degree of broiler feathering in the usual late-feathering stock of the Rhode Island Red breed. An unselected strain of Single-Comb Rhode Island Red was used for most of the physiological studies.

FEATHER TRACTS

For the purpose of this study, 10 feather tracts are recognized. The name given to the tract is indicative of its location, which is shown in figure 1.

The differentiation among the birds used in this study was based on the condition of feather development at the end of the seventh or eighth week. An arbitrary scoring system was devised, and in esti-

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[2] Acknowledgment is due Dr. J. S. Hughes of the Chemistry Department and to Dr. Mary T. Harman of the Zoology Department for aid in special phases of the work.

mating the feathering of a bird by this system each of the 10 feather tracts was individually graded. A maximum grade of three points was assigned to each of these tracts. In order that a tract might receive the perfect score of three points, the feathers growing thereon must have been sufficiently long and abundant to cover completely the whole area of the tract. A tract with feathers abundant but not quite long enough to exhibit a uniform surface was cut one point. A tract was cut two points if the feathers were sparsely scattered over the tract, many in the pin stage, and areas free from feathers were showing. If no feathers had appeared, and the down still persisted, a tract was given a score of zero. Thus a bird with well-developed feathers on all of its 10 tracts might make a maximum grade of 30

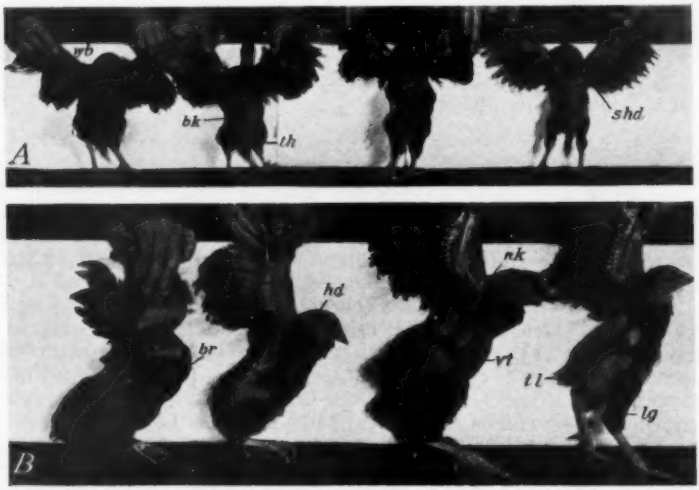

FIGURE 1.—Variations in degree of feathering and location of feather tracts: *A*, Dorsal view: *wb*, Web; *bk*, back; *th*, thigh; *shd*, shoulder. *B*, Lateral view: *br*, Breast; *hd*, head; *nk*, neck; *vt*, ventral; *tl*, tail; *lg*, leg.

points. Figure 2 shows representative skin samples from the back region of 7-week-old birds with scores of 0, 1, 2, and 3.

In the early work, the evaluation of feathering was made at 8 weeks of age. In the later investigations, however, it was made at 7 weeks. This change was deemed advisable, because it was found that the difference in the degree of feather growth among birds was obscured with advancing age. Thus, the variability among such birds was more strikingly evident at about the seventh week of age. Since considerable sexual dimorphism exists in relation to rate of feathering, it was impossible to select an age which would be optimum for both sexes. The age of 7 weeks was perhaps a little late for females, but a younger age would have been too early for the most satisfactory classification of males.

PHYSIOLOGICAL STUDIES

A number of different studies have been made during the course of this investigation with a view to ascertaining the physiological nature

of feathering. Dietary, hormonal, as well as environmental, agents have been studied in their relation to feathering. In the discussions which follow, the question of interrelationship among the various agents studied will be pointed out in the light of the results secured.

FEATHER GROWTH

The process of feather development has been studied by a number of workers; therefore, it is not necessary to go into the details at this time. However, a brief description of the more important steps leading to the formation of the feathers seems pertinent. Feathers first appear as small papillae on the skin of the embryo about the sixth day of incubation. These papillae, which arise from the epidermal layer of the skin, elongate and at the same time tend to sink

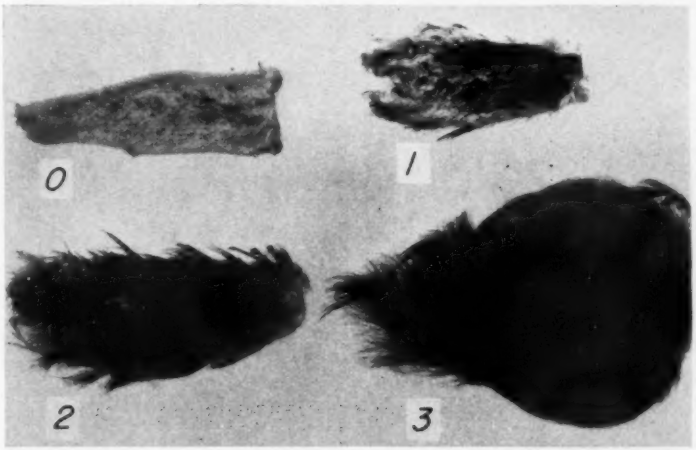

FIGURE 2.—Representative skin samples from the back region of 7-week-old birds with scores of 0, 1, 2, and 3.

below the surface into the dermis to form the feather follicles. According to Hosker (*8*),[3] the down and the definitive feathers arise in a similar manner from the stratum Malpighii of the skin and the papilla, respectively.

The definitive feather develops from the same papilla from which its downy predecessor had arisen, and at the time the definitive feather appears externally the interior end of the down is often attached to the tip of the newly formed feather.

A wide range of variation exists as to the time of appearance of feathers. Some chicks are practically fully clothed with feathers at 4 weeks of age, while others carry the juvenile down for as much as 12 weeks. The question arises as to what is the status of the feather in the birds in which this long-delayed emergence occurs.

Histological studies were made on skin from the backs of 7-week-old birds which were entirely devoid of feathers and comparison was made of skin from the back region of day-old chicks. The only difference observed was that the feather follicles in the 7-week-old bird appeared

[3] Reference is made by number (italic) to Literature Cited, p. 704.

deeper and larger than those in the day-old chick. This condition was evidently due to the relative thickness of the skin in the two birds rather than to further differentiation having occurred in the older bird.

The stage of development at which delay in feather development occurs seems to be the very initial stage in formation marked by the proliferation of the intermediate cells. No indication of this cellular proliferation was noted in the transverse skin sections of the 7-week-old birds which were studied. The histological picture of the inactivated feather germ to which the down is still attached, as found in a 7-week-old Rhode Island Red bird, is shown in figure 3. This figure

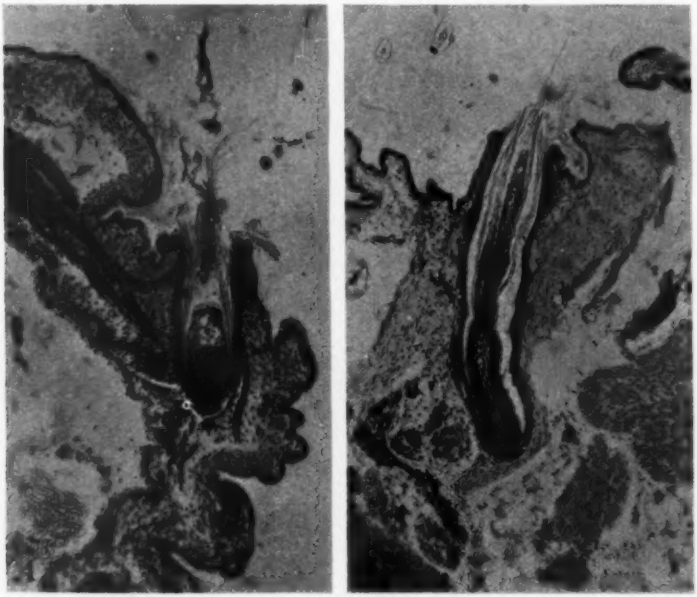

FIGURE 3.—Development of the feather. *A*, Transverse section of a feather follicle from the back region of a day-old chick. × 200. Implantation of the down in the follicle is evident. *B*, Transverse section of a feather follicle from the featherless back of a 7-week old chick. × 200. Note the persistence of the juvenile down and the similarity to the day-old chick follicle with respect to lack of cellular differentiation within the follicle. The feather follicles of this bird are deeper, because of its thickened skin.

also shows the details of the feather germ as it exists in a day-old chick of the same breed.

ORDER OF APPEARANCE OF FEATHERS IN THE TRACTS

The age at which the feathers begin to appear on the various tracts of a single bird differs as much as 8 weeks. The feathers located at the caudal end of a tract usually appear first and attain the greatest length.

A systematic study was made of the order of appearance of feather tracts. The chicks were examined at weekly intervals. The data obtained on the three strains of Rhode Island Reds used in this study are given in table 1. The data show the age at initial appearance of feathers in a tract and also variability in time of appearance. Similar data on the early- and late-feathered strains of White Leghorns are also shown in table 1.

The number of chicks in each sex in the various strains shown in table 1 ranged from 24 to 46. It should be kept in mind that the early-feathered Leghorns and the well- and poor-feathered Rhode Island Reds constitute the normal condition for these two breeds. The sex-linked early-feathered strains in the two breeds show an earlier development of feathers in most tracts than do the other strains. This is most strikingly exhibited in the tail tract.

TABLE 1.—*Time and order of appearance of feathers in the different tracts in early-, well-, and poor-feathered Rhode Island Reds and early- and late-feathered White Leghorns*

RHODE ISLAND REDS

Tract	Strain	Percentage distribution of birds on basis of age at time of appearance of tract															
		Males								Females							
		1 week	2 weeks	3 weeks	4 weeks	5 weeks	6 weeks	7 weeks	8 weeks	1 week	2 weeks	3 weeks	4 weeks	5 weeks	6 weeks	7 weeks	8 weeks
Tail	Early	100								100							
	Well				13	61	18	4	4			8	63	29			
	Poor				13	33	7	20	27				20	20	27	27	6
Shoulder	Early	100								100							
	Well	12	36	36	12	4				17	79	4					
	Poor	6	27	7	27	13	13		7	33	20	13	27	7			
Thigh	Early	61	39							58	42						
	Well			60	32	8					13	83	4				
	Poor			20	47	20	7		6		7	40	20	27	6		
Breast	Early	13	87							21	79						
	Well			68	20	12					25	69	6				
	Poor			60	33	7					27	67	6				
Neck	Early		96	4							96	4					
	Well			4	40	36	16		4			13	70	16			
	Poor				13	33	7	27	20				20	40	40		
Back	Early		74	22	4						79	21					
	Well				8	46	29	13	4			8	46	42	4		
	Poor					7	13	40	40				13	27	33	20	7
Web	Early		92	4	4						92	8					
	Well				4	29	46	13	8				25	67	8		
	Poor						33	33	34				7	13	67	13	
Leg	Early		22	74	4						29	67	4				
	Well				71	17	12					17	75	8			
	Poor			7	73	20						33	60	7			
Ventral	Early			26	52	22						29	63	8			
	Well					41	41	14	4			4	21	63	12		
	Poor					7		53	40				6	27	40	20	7
Head	Early			9	83	8						29	63	8			
	Well				16	44	28	12				4	42	38	16		
	Poor				13	60	13	7	7				13	80		7	

WHITE LEGHORNS

Tail	Early	100								100							
	Late		12	6	70	12				7	33	33	27				
Shoulder	Early	100								91	9						
	Late		29	29	24	18				13	53	27	7				
Thigh	Early		89	11						9	82	9					
	Late		6	71	23						13	74	13				
Breast	Early		89	11						9	82	9					
	Late		6	71	23						20	73	7				
Neck	Early		11	83	6							100					
	Late			6	94							14	86				
Back	Early		11	72	17							82	18				
	Late			12	35	35	18					27	67	6			
Web	Early		6	72	22							82	18				
	Late				24	53	23					7	67	26			
Leg	Early			17	78	5						9	91				
	Late				88	12						13	80	7			
Ventral	Early			6	83	11							91	9			
	Late				41	53	6						93	7			
Head	Early			6	50	44							73	27			
	Late				24	76							60	40			

The order of appearance of the tracts varied somewhat in the different strains but usually the shoulder, thigh, and breast were the first regions to show feather development.

The various strains differ consistently enough to indicate that in addition to the well-known sex-linked pair, other genetic factors control the time of appearance of the adult type of plumage. The later classification as to feathering at 7 and 8 weeks is probably a measure of the same genetic differences noted here.

EFFECT OF BODY GROWTH ON RATE OF FEATHERING

The influence of body weight upon the rate of feathering at 8 weeks has been studied. It appears from the results of this study, which was carried out on unselected Rhode Island Red birds, that the influence is not great. The coefficient of correlation between body weight and grade of feathering was found to be 0.194 ± 0.013 and 0.055 ± 0.016 in 305 males and 297 females, respectively. These values are too low to be of any practical importance.

The analysis of data obtained from a similar study in 1933 gave somewhat higher correlation coefficients, these being 0.2398 ± 0.0359 in 312 males and 0.3833 ± 0.0336 in 292 females. Gericke and Platt (*6*) in work with Barred Plymouth Rocks secured a coefficient of correlation of 0.8120 ± 0.0109 between body weight and feather development when the chicks were 8 weeks old. It should be noted, however, that these investigators raised their birds on rations of different protein levels, which might have been a factor in securing such a high correlation value. In the present studies all the birds were given a normal ration and management. Jaap and Morris (*9*), working with a number of different breeds of fowl, reported a correlation coefficient of 0.23 between body weight and feathering at 8 weeks.

It thus appears from these studies that body weight and feathering as determined at the age of 8 weeks bear no close relationship.

SEX IN RELATION TO FEATHERING

Sexual dimorphism in rate of feathering was noted throughout this investigation. Table 1 gives a comparison of time of appearance of feathers in the various tracts of birds of the different strains studied. In this table is given the percentage of chicks showing each feather tract at ages ranging from 1 to 8 weeks. The data clearly demonstrate sexual dimorphism in the rate of feathering. A comparison of the males and females of any one strain shows an earlier appearance of the tract in the case of the females, or a higher percentage of the females showing feathering in a given tract at any period.

Studies made on the development of the embryonic feather papillae in connection with this investigation revealed that in the female chick embryo the feather papillae appear somewhat earlier than in the male embryo, the difference in time of appearance between the two sexes being only a matter of a few hours. On the basis of this fact, it was possible to distinguish the sex of the embryo by the relative development attained in its feather germs. The results of this phase of work are not yet published.

From the foregoing discussion, it is evident that feathering is greatly affected by sex, since the time of appearance of feathers and their rate of growth seem to be closely associated with sexual phe-

nomena. As a rule, the feathers of the female appear earlier and grow at a higher rate than those of the male.

MOLT IN RELATION TO BROILER FEATHERING

Molt is known to take place in the growing chick as well as in the adult bird. Marble (*14*) observed that at 6 weeks of age the White Leghorn female chicks showed considerable molt in neck, back, pelvic wing (thigh), and pectoral (breast) regions, while no molt was evident in the males of the same age. During the seventh and eighth weeks, he observed that this molt continued to show more distinctly, in the female alone. Dunn and Landauer (*5*), working on the Silver-Spangled Hamburg, reported that the process of molt occurs in a definite rhythm in a given feather tract and is almost continuous during growth. Warren and Gordon (*22*) noted that in the Rhode Island Red and Leghorn breeds, as well as in other domestic fowls, the juvenile remiges undergo at least one complete molt during growth.

The effect of molt in the growing chick on the feathering score as determined in this study was of interest. Eight Rhode Island Red and eight White Wyandotte chicks were dipped in a coloring solution of crystal violet when 3 weeks of age. The White Wyandottes were used primarily because of the advantages of dyeing a white plumage.

Weekly observations were made on all the feather tracts of these chicks to ascertain whether molt had occurred. The fact that in the majority of individual tracts the feathers make their appearance in a definite succession, namely, the postero-anterior direction, was of some aid in the search for the molted feathers. The presence of an undyed feather among the feathers of dyed tips was indicative of molt.

At the age of 6 weeks, by which time practically all the feather tracts had made their appearance, the chicks were dipped in a green dye. The green color, however, was not sufficiently dense to mask the purple used in the previous dyeing.

The results of this study indicate that molt previous to 9 weeks of age is not a factor of importance in broiler feathering. No indication of molt was observed during the first 7 weeks of this experiment, and only slight evidence of molt was noted at 9 weeks. It is clear that the first molt in Rhode Island Reds and Wyandottes takes place later than in the Leghorns in which Marble (*14*) found molt occurring at 6 weeks of age. The findings also show that molt does not materially affect the results of this study.

RELATION OF DEGREE OF FEATHERING AT EARLIER AGES TO THE FEATHERING SCORE

Length of Wing Feathers of Day-Old Chicks and the Feathering Score

One of the problems considered during the course of this investigation was to determine the relationship between the growth rate of the primary wing feathers and the feathering condition of the bird at 8 weeks. The primary wing feathers are the first definitive feathers to appear on the chick of the domestic fowl. As a rule, these feathers are present when the chick hatches.

All the Rhode Island Red chicks that were hatched during the season of 1934 were examined on the day of hatching to determine the relative length of the wing primaries. This stock did not carry the sex-linked early-feathering factor. These chicks were classified

into two arbitrary groups according to the length of their primary feathers. Those which had long primaries (approximately one-half inch) comprised one group and those which had short primaries (approximately one-third inch) comprised the other. At 8 weeks of age, the degree of feather growth was determined according to the scoring scale previously described.

From the results secured, the length of primary wing feathers at hatching does not seem to bear any relation to the 8-week feathering condition. The 8-week mean feathering scores of 210 males and 220 females which had, as baby chicks, long primaries, were 23.8 and 27.6 points, respectively. On the other hand, the mean scores of 95 males and 77 females designated as having short primaries when they were 1-day old were 22.2 and 27.0 points, respectively. The lack of difference between these two groups of birds may be ascribed to the influence of the time elapsing since hatching. The chicks that emerged from the shell first are most likely the ones which were classed as having longer primaries, while those that hatched late are probably the ones which had short primaries and, therefore, were designated as such. At any rate, the results indicate that this measure of variability is not to be relied upon for the purpose of prediction.

Number of Primary Wing Feathers in Day-Old Chicks and the Feathering Score

The number of primary wing feathers present in day-old chicks was studied in relation to 7-week feathering score. As previously stated, the wing primaries are the first definite feathers to appear on the chick. The number of these feathers present at the time of hatching is subject to considerable variation, even among birds of the same strain.

The observations upon which this study was based were made on a group of Rhode Island Red chicks hatched from an unselected population known to carry the sex-linked late-feathering factor. At the time of hatching, the chicks were examined and the number of primary wing feathers present was recorded. These chicks were reexamined at the age of 7 weeks to determine the degree of development attained by their feathers. The data secured from observations made on 731 birds, including 271 males and 460 females, were tested for the degree of association between the number of primary wing feathers present at the time of hatching and the 7-week feathering score. The coefficient of correlation secured was 0.2038 ± 0.039 in the males, and 0.2774 ± 0.029 in the females. These correlation values indicate that the two variables considered are significantly associated with each other. As a practical basis of prediction, however, the value of correlation is low.

Length of Wing Feathers of 13-Day-Old Chicks and the Feathering Score

Another point of interest is the relationship between the length of wing feathers at 13 days of age and the 8-week feathering score. In this experiment, the birds were examined on the thirteenth day of age and the length of the wing feathers was noted in comparison with the length of the body. The length of the wing feathers at this stage of development varied considerably. Some birds had wings the tip of which when folded reached approximately half the

length of their bodies, while in other birds these feathers were as long as seven-eights of the body.

The birds were classified into four groups, according to the relative length of their wings. These groups were designated as ½, ⅞, ¾, and ⅞, in comparison of the wing with body length. At the termination of the experimental period of 8 weeks, and after the birds had been graded according to the scoring scale previously mentioned, they were classified into these four different groups based on wing length and the mean 8-week feathering score of each of the four groups was determined. The results of the classification of 305 males and 297 females are summarized in table 2.

TABLE 2.—*Relation of length of primaries in 13-day-old chicks to the degree of feathering at 8 weeks of age*

Sex	Mean 8-week feathering score for birds having indicated length of wing at 13 days			
	½ body length	⅝ body length	¾ body length	⅞ body length
Females	26.38	27.66	28.27	29.00
Males	22.45	23.93	26.85	

The data in this table show that the longer the wing in relation to length of body at 13 days of age, the better the feathering at 8 weeks, and vice versa. This fact might be utilized as an index for evaluating the future feathering of the bird.

In connection with this study, the coefficient of correlation between 3-week and 8-week feathering was also determined on 254 males and 272 females. The correlation values were 0.5896 ± 0.0276 and 0.5840 ± 0.0269 in the males and females, respectively. These values indicate a rather high degree of association between the feathering condition of the two ages considered.

NUTRITIONAL STUDIES

No exhaustive nutritional studies were planned; only those dietary factors were investigated that seemed to bear directly on the problem. The nutritional tests were made with Rhode Island Reds, previously unselected for feathering condition. The type of feathering found in these birds is very similar to that commonly present in most of the larger breeds of fowl. This stock was known to be homozygous for the sex-linked late-feathering factor. Numerous studies (*15*, *17*, *19*, *24*) have been made of the vitamin A requirements of the chick, but little attention has been given to the influence of the level of this vitamin on chick feathering. Three lots of birds, each consisting of 49 Rhode Island Red chicks, were used in this experiment. The chicks in this and other nutrition experiments were kept in battery brooders. To each of the three lots the following basal ration was fed: 37 pounds ground white corn, 16 pounds wheat shorts, 16 pounds wheat bran, 16 pounds ground oats, 15 pounds meat meal, and 1 pound salt.

In addition to this ration, vitamin A was supplied in the form of a commercial concentrate which, according to the manufacturer, con-

tained 1½ million International units of vitamin A per pound. The number of units of vitamin A fed to each of the three lots was 1,160, 3,311, and 5,291 per pound of feed. To avoid the loss of vitamin A potency only enough mash was mixed at a time to carry a lot of chicks for a week. It may be noted that the use of subminimal quantities of vitamin A would have been inadvisable in an experiment of this nature, since the retardation of body growth might affect the growth of feathers.

Vitamin D was also supplied the chicks in the form of concentrate.

The results of this experiment (table 3) seem to indicate that vitamin A in the quantities here used is not an important factor in feather growth. The analysis of variance (*18*) showed that variations in feathering due to the different levels of vitamin A used were too low in the female to be of significance. In the males, however, the variations closely approached the point of significance. The ratio of the variance between the means of the three vitamin levels to that of the experimental error, commonly designated as F, is 2:10, while the expectation of random sampling on the basis of 5 times in 100 trials is 2:14. Therefore, vitamin A in the quantities fed in this study was of questionable value in promoting feather growth.

TABLE 3.—*The average 7-week feathering grade and body weight of 3 lots of chicks fed different quantities of vitamin A*

Lot No.	Vitamin A per pound of feed	Males			Females		
		Chicks	Mean feathering score	Mean body weight	Chicks	Mean feathering score	Mean body weight
	International units	*Number*		*Grams*	*Number*		*Grams*
1	1,160	22	6.4	332.7	18	9.0	323.8
2	3,311	26	7.1	352.7	19	9.9	323.7
3	5,291	20	8.0	343.5	20	8.7	295.0

Grains and their byproducts make up the major part of the poultry ration. It is therefore desirable to know the extent to which the various grains affect the growth of feathers at the broiler stage of development.

Branion (*1*) investigated the role of corn, wheat, oat groats, and barley in poultry nutrition and found that chicks raised on a high intake of corn did not grow feathers over the back and their feather development was generally retarded. In a study to determine the comparative value of ground oats and wheat products in chick feeding, Wilcke (*23*) reported that the chicks raised on a ration consisting of 72 percent of ground oats had normal growth and excellent feathering. He also reported that the chicks raised on a ration consisting of 72 percent of ground yellow corn made poor growth and their feathering was of poor quality.

Three of the most widely used grains in poultry feeding, namely, corn, wheat, and oats, were chosen for this test. Four groups of birds, each consisting of 56 Rhode Island Red chicks, were used. One group each was fed exclusively on either corn, wheat, or oats. The fourth group was given a combination of the three grains. A basal mixture consisting mainly of concentrates was fed to all chicks in

addition to these grains. This mixture consisted of 7 parts meat scrap (high grade), 8 parts dried buttermilk, 5 parts alfalfa leaf meal, 1 part salt, and 1 part cod-liver oil.

Equal quantities of the basal mixture were used in making up the mash fed to the four lots of chicks. Likewise, the total crude protein in each of the four rations was kept equal and uniform throughout the test. The composition of the four rations used in this study is given in table 4 and a summary of the results secured is given in table 5.

TABLE 4.—*Composition and the total crude-protein content of rations used for comparison of influence of various cereal grains on feathering*

Ingredient	Rations used for—							
	Lot No. 1		Lot No. 2		Lot No. 3		Lot No. 4	
	Constituents	Crude-protein content	Constituents	Crude-protein content	Constituents	Crude-protein content	Constituents	Crude-protein content
	Pounds	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*
Basal mixture	22.0	8.34	22.0	8.34	22.0	8.34	22.0	8.34
Ground yellow corn	70.5	6.55					23.5	2.34
Ground whole wheat			78.0	9.59			26.0	3.20
Ground oats					78.0	9.75	26.0	3.25
Corn gluten meal	7.5	2.86					2.5	1.02
Total	100.0	17.75	100.0	17.93	100.0	18.09	100.0	18.15

TABLE 5.—*Effects of various grain rations shown in table 4 on feathering and growth*

Lot No.	Grain	Birds	Sex	Mean feathering score	Mean body weight
		Number			*Grams*
1	Corn	34	Male	7.0	368.2
		21	Female	10.3	359.5
2	Wheat	26	Male	7.9	380.3
		21	Female	10.7	346.2
3	Oats	20	Male	8.8	447.5
		24	Female	10.0	375.8
4	Mixture of corn, wheat, and oats.	26	Male	7.5	436.5
		20	Female	10.6	407.5

Table 5 shows that the males of lot 3, raised on the oat ration, made the highest feathering score and gained the most in body weight. The females of the same lot did not show any improvement in their feathering over those of the other lots, but they showed a better gain in body weight than was made by lots 1 and 2. Lot 4, for which a mixture of the three grains was used, made the most rapid gain in body weight.

Lot 3 had the highest mortality, 23 percent at 7 weeks of age. Mortality in lots 1, 2, and 4, was 1.8, 16.0, and 17.8 percent, respectively. Some perosis occurred among the chicks which were on a corn ration.

The data were subjected to analysis of variance, and the variations in feathering due to differences in the composition of ration were not large enough to have statistical significance. The ratio of the variance between the means of the 4 rations to that of the experimental

error is 1.84, while the expectation of random sampling on the basis of five times in 100 trials is 2.7.

In the nutritional studies, the effects of vitamin G (B_2) and protein level of the ration on the growth and development of feathers were also tested. In this test, four rations in which the percentage of protein varied from 11 to 25 were used. Widely different ranges of vitamin G were maintained in these rations. Although as a result of disease, the number of birds utilized in this test was not sufficiently large to permit any definite statement regarding the role of either protein or vitamin G in the growth of feathers, the results seemed to indicate that both of these nutrients are of some importance in this respect. The variations in feathering due to feeding different levels of protein were more significant than those ascribed to the vitamin G content of the ration.

Two other studies of nutritional interest were also made for the purpose of testing the effects of magnesium carbonate and cystine on the growth of feathers. In neither of the two tests was the number of birds large enough to warrant a definite conclusion. However, the results seemed to indicate that feeding a standard poultry ration supplemented with 3 percent of magnesium carbonate or 0.5 and 1 percent of cystine in no way influenced feather growth.

ENDROCRINOLOGICAL STUDIES

Activity of the Thyroid Gland in Relation to Feathering

Various studies (*4*, *12*) have been attempted to discover the role of the thyroid of the fowl in relation to body size, egg production, sexual activity, plumage structure, and pigmentation of feathers, as well as to many other physiological phenomena. Schwarz (*16*) observed that in thyroidectomized birds, feather growth was inhibited. He concluded that the increase in thyroid activity accelerates feathering. Hardesty (*7*), who studied the effect of thyroxine injections upon the feathers of guinea fowl, has stated that thyroxine, even in small doses, abruptly stimulates the germ lying quiescent in the follicle. She also noted that without exception feathers treated with thyroxine reach maturity at an earlier age than do controls from the same follicles. Chaudhuri (*2*) found that the iodine content of the thyroid of sexually immature males is lower than that of the thyroid of mature males. He, however, found no indication of sexual dimorphism with respect to the iodine content of this gland. Cruickshank (*3*) corroborated the findings of Chaudhuri regarding the increase in iodine content in the thyroid of the male with the advance in age. In his biochemical studies on the epidermal structures of mammals and birds, Kosjakoff (*11*) reported that generally more iodine is found in the feathers and hairs of the female than in those of the male.

Two groups, an experimental and a control, each consisting of 20 late-feathering Rhode Island Red chicks were used in this investigation. Since it was desirable to have the two groups of chicks as nearly identical as possible, they were selected as pairs, each pair chosen to match as perfectly as possible in body size and degree of feather growth on the various tracts. At the age of 3 weeks a condition of hyperthyroidism was artifically induced in the chicks of the experimental group by injecting into the pectoral muscles of each chick 0.5 mg of crystalline thyroxine dissolved in 0.5 cc of distilled water. The

experimental and control chicks were kept together in an electric battery brooder, insuring similar environmental conditions.

Preliminary results showed that there was no difference with respect to feather growth among the birds repeatedly injected with thyroxine and those that received a single injection.

The results of this study are summarized in table 6. The experimental group made a higher mean feathering score than the controls. In only one case, male No. 2806, did the administration of thyroxine fail to induce improvement in the feathering over that found in the other member of the pair. The mean feathering score of the birds injected with thyroxine was 14.8 points for the males and 25.2 points for the females. On the other hand, the birds which received no thyroxine scored 10.0 and 20.0 points for the males and the females, respectively. With respect to body weight birds of the same sex in the experimental and control groups were very similar. It thus appears that the increased thyroid activity of the bird leads to a stimulation in the rate of its feather growth.

It is to be concluded from this study that the administration of thyroxine into Rhode Island Red chicks at the age of 3 weeks caused the feathering of both male and female chicks to be accelerated.

TABLE 6.—*Influence of thyroxine injection on feather growth*

Experimental group				Control group			
Sex and chick No.	3-week weight	7-week weight	Feathering score	Sex and chick No.	3-week weight	7-week weight	Feathering score
Male:	*Grams*	*Grams*		Male:	*Grams*	*Grams*	
2797	160	410	14.5	2868	160	560	11.0
2804	170	540	12.5	2786	180	500	12.0
2806	100	340	3.0	2833	100	350	9.0
2811	190	580	24.5	2852	190	520	12.0
2820	170	470	19.0	2860	170	540	11.5
2838	190	550	17.5	2874	190	620	17.0
2844	185	480	17.0	2828	190	600	9.0
2845	150	440	10.0	2863	160	560	8.5
2851	180	600	16.5	2861	180	450	13.0
2866	100	450	14.0	2876	90	340	6.5
2867	130	420	17.0	2826	130	440	7.5
2871	150	550	13.0	2878	150	300	3.0
Mean		485.5	14.8	Mean		481.6	10.0
Female:				Female:			
2788	180	550	24.5	2791	180	530	18.5
2793	180	420	20.0	2792	190	580	18.0
2799	170	370	28.0	2882	160	520	23.5
2810	180	600	25.5	2884	190	460	21.0
2812	160	440	23.0	2842	170	340	15.0
2832	220	560	27.0	2897	210	640	24.5
2856	200	540	27.0	2886	190	520	17.5
2996	210	520	26.5	2873	210	560	22.5
Mean		500.0	25.2	Mean		518.8	20.0

EFFECT OF IODINE ON GROWTH OF FEATHERS

The effect of iodine on the growth of feathers was tested by feeding 21 birds, of which 14 were males and 7 were females, a standard ration to which potassium iodide was added at the rate of 1.5 g per 100 pounds of feed. The mean feathering score of the males at the age of 7 weeks was 13.5, while that of the females was 21.6. In another group of birds which were kept as controls 9 males had a mean feathering score of 10.4 while 9 females had a mean score of 18.9. Although

the number of birds employed was not large enough to warrant definite conclusions with respect to the role of iodine in the growth of feathers, the results indicated that iodine has some stimulating effect on feather growth. However, this effect was more markedly expressed in the male than in the female.

EFFECT OF ENVIRONMENT ON GROWTH AND DEVELOPMENT OF FEATHERS

Humidity

It is a common belief among poultry producers that high humidity in the brooding room is conducive to better feathering. Although high humidity is recommended as one of the requirements for successful brooding, no experimental evidence in support of this view has been found. An experiment was accordingly undertaken to ascertain the extent to which humidity is a factor in broiler feathering.

One lot of 60 Rhode Island Red chicks was raised in a relatively dry basement room while another comparable group was housed in a humid one. All chicks were kept in a frame structure made of wire and elevated about 3 feet from the floor to permit free circulation of air. In the dry room, no liquid material other than water was present and droppings were removed daily to restrict evaporation. The floor and walls of the humid room were thoroughly moistened several times during the day and evening. A fine mist spray operating continuously in the room saturated with water a large piece of burlap hanging from the ceiling. Temperature and humidity in both rooms and outdoors were recorded each morning and afternoon. A sling psychrometer was used for taking humidity readings. Efforts were made to maintain the same temperature in the two rooms. The mean morning and afternoon temperatures of the humid room for the duration of the experiment were $79.4° \pm 0.56°$ and $83.3° \pm 0.40°$ F., while those of the dry room were $81.5° \pm 0.49°$ and $84.4° \pm 0.39°$.

The mean relative humidity in the humid room for the duration of the experiment was found to be 72.2 percent in the morning and 69 in the afternoon, as compared with 51.8 and 50.7 in the dry room. The outside atmosphere was more humid than that of the dry room, but considerably less so than that of the wet room.

All chicks were fed a growing ration containing about 18 percent of protein, and except for humidity were treated alike. At the close of the seventh week the birds were weighed and graded for feathering.

The results of this experiment (table 7) indicate that higher humidity favors feather growth but that it has no effect on body weight.

TABLE 7.—*Influence of humidity on feathering*

Humidity	Mean relative humidity		Mean temperature		Birds	Sex	Mean feathering score	Mean body weight
	A. M.	P. M.	A. M.	P. M.				
	Percent	*Percent*	*° F.*	*° F.*	*No.*			*Grams*
High	72.2	69.1	79.4	83.3	31	Male	12.3	490.0
					22	Female	18.2	453.1
Low	51.8	50.7	81.5	84.4	32	Male	11.1	464.6
					20	Female	15.8	459.5

The analysis of variance shows that the ratio of the variance between the means of the two groups of birds to that of the experimental error, commonly referred to as F, is 6.02, while the expectation of random

sampling from a homogenous population is only 3.94, thus indicating that the difference in feathering is statistically significant.

TEMPERATURE

Although no critical experiments on the subject could be found, one frequently finds the statement that too high brooding temperatures tend to retard feather growth. Kleiber and Dougherty (*10*) have conducted an extensive investigation on the effect of environmental temperature on the utilization of food energy in the White Leghorn chick. They reported that the daily rate of growth was increased when the environmental temperature was decreased. Likewise, the chicks raised at 21° C. were found to have a much higher basal metabolism than those raised at 40°. In another study made by Landauer (*13*) on the relation of thyroid gland activity to environmental temperature in the Frizzle fowl, it is reported that a change in the environmental temperature resulted in a corresponding change in the activity of the thyroid gland, which consequently led to similar changes in the metabolic rate of the bird.

Two groups of 90 Rhode Island Red chicks were kept in adjacent basement rooms of equal size. The chicks in the high-temperature room were supplied heat from an electric hover placed on the floor, and in addition the entire room was heated by a gas stove to a temperature averaging 85° F. throughout the period of the experiment. The chicks in the low-temperature room were provided an electric hover but no supplementary heat. Thus the room was kept fairly cool (68°) except under the hover, which remained just warm enough to supply the chicks with the necessary heat. In the low- temperature room the temperature under the hover was gradually reduced and during the last half of the experiment the current was shut off. In this room the mash hoppers and the water fountains provided were placed at a distance from the hover in order to induce the chicks to spend as much time as possible away from the heat of the hover. Temperatures were recorded twice daily 6 inches from the floor both under and outside the hovers.

The two lots were fed the regular Kansas State College growing mash and a record of the amount of feed consumed by each lot was kept. At the close of the seventh week, individual weights were taken and the degree of feathering was evaluated.

The results of this experiment (table 8) indicate that low temperature has a stimulating influence on feather growth. The influence of the environmental temperature was more evident in the females, the improvement in feathering of females being 28.5 percent and that of males 19 percent.

The analysis of variance shows that the variation in feathering due to differences in environmental temperature is highly significant. The ratio of the variance between the means of the two groups to that of the experimental error is 47.3, while the expectation of random sampling on the basis of once in 100 trials is only 6.81. It is to be noted that feathering here was much better in both groups than in other experiments. This might have been due to the fact that the birds used in this study were given access to the entire floor of the room, whereas in the other experiments the chicks were raised in battery brooders.

TABLE 8.—*Influence of brooding temperature on feather and body growth*

Temperature	Mean temperature		Birds	Sex	Mash consumed per chick	Mean feathering score	Mean body weight
	Hover	Room					
	°F.	°F.	*Number*		*Pounds*		*Grams*
High	88.6	85.0	44	Male	2.74	12.1	571.6
			42	Female		15.4	506.0
Low	81.9	68.3	36	Male	3.01	14.4	563.3
			41	Female		19.8	541.2

Mortality was somewhat higher among the chicks raised in the cold room than among those in the warm room, being 14 and 4 percent, respectively. The increased mortality among chicks raised in the cold room may have been due to the rather cool environment in which they were compelled to live. The chicks in the cold room consumed more feed than did those in the warm room. This observation confirms the findings of Kleiber and Dougherty (*10*). The chicks in the cold room were more active than those in the warm room. In a number of instances the birds in the cold room actively engaged in a search for food, while those in the warm room squatted lazily on the floor. Thus increased exercise may have been responsible for increased food consumption and a resulting acceleration of metabolism.

CONCLUSIONS

Vitamins A and G have been found to be of questionable value in promoting the growth of feathers. Oat feeding produced feathering of questionable superiority as compared to corn and wheat.

Low brooding temperature and high humidity were shown to be of importance in bringing about better feathering. Landauer (*13*) has found that a condition of hyperthyroidism prevails in chicks kept at a low temperature, and since an induced hyperthyroidism results in better feathering as found in the experiment on thyroxine, it appears that the improved feathering in the chicks raised at a low temperature bears a relation to the functioning of the thyroid gland in these birds. The feeding of iodine seemed to make some improvement in feathering.

There is evidence in several experiments that the males are more responsive than the females to changes in diet, when measured by feather growth. There is probably no sexual dimorphism as to responsiveness, but this apparent difference is due to the fact that at the age of examination the males were at a more critical stage. The females were probably a little beyond this stage and the results were less evident. Body molt was not a factor of importance in feathering as considered in these studies.

GENETIC STUDIES

The genetic phase of the work consisted of studies of the hereditary nature of feathering in its diverse types as these occur in the Rhode Island Red and White Leghorn breeds.

Since the hereditary behavior of early and late feathering, ordinarily present in the so-called light and heavy breeds of the domestic fowl, respectively, is well understood, particular attention was given throughout this work to the nature of variations found in a strain of the Rhode Island Red breed, known to be homozygous for the dominant sex-linked late-feathering character. An attempt also was made to establish by selection in opposite directions, extreme types of

feathering in the Rhode Island Red. Various crosses have been made between the different types of feathering found in the Rhode Island Red and White Leghorn to ascertain whether feathering in the two breeds has the same genetic basis.

BREEDING LINES

Three strains of the Rhode Island Red breed, namely, the early-feathering, the poor-feathering, and the well-feathering, and two strains of the White Leghorn breed, early- and late-feathering, were used in this work. The establishment of these strains was accomplished through breeding and selection over a period of years.

The White Leghorn fowl is ordinarily classed as an early-feathering bird, in which feather growth is known to be controlled by a recessive, sex-linked gene (*20*). The so-called late-feathering White Leghorns, carrying the dominant allel of early-feathering, do not commonly exist in this breed. This strain was developed at the Kansas station by first outcrossing to Barred Plymouth Rocks and then repeatedly backcrossing the resulting offspring to White Leghorns. By such a procedure it was possible to establish a strain breeding true for nearly all of the Leghorn characteristics but possessing the sex-linked late feathering of heavy breeds.

The Rhode Island Red breed is ordinarily homozygous for the sex-linked late-feathering. However, considerable variation occurs in the rate of feathering of Rhode Island Reds carrying the late-feathering factor, and these variations were the sources of material for selection in the well- and poor-feathered strains. There was considerable overlapping of extremes of these two strains, but as data presented later will indicate, significant differences were established by selection.

The so-called early-feathering Rhode Island Reds were of a strain homozygous for the sex-linked early-feathering gene. Such individuals occasionally are found in pure-breeding stock of Rhode Island Reds and the mating of such individuals established this strain. The early-feathering Rhode Island Reds were much like ordinary White Leghorns in the rate of feather growth. In contrast to most other Rhode Island Reds, the chicks of both sexes are practically fully covered with feathers at 4 weeks of age.

The well- and poor-feathered Rhode Island Reds and the late-feathered White Leghorns have the same genetic constitution in that each carries the sex-linked late-feathering gene. The early-feathered Rhode Island Reds carry the sex-linked recessive gene for early-feathering which is characteristic of ordinary White Leghorns. Any differences in feathering of these strains at the broiler stage gradually disappear and are entirely eliminated at sexual maturity.

INFLUENCE OF SELECTION IN WELL- AND POOR-FEATHERED STRAINS OF RHODE ISLAND REDS

During the course of this study, an attempt was made to produce extreme types of well- and poor-feathered Rhode Island Red birds. This was done by selecting as breeders the best-feathered birds in the well-feathered strain and the slowest feathering ones among the poor-feathered strain. The progeny test was emphasized in the selection work. Not only was the individual feathering graded, but the family averages were also given consideration in the choice of breeders in each generation. In order to maintain satisfactory viability in the

stock, some attention was given to the vigor of birds mated and in some instances sacrifices were made in feathering grade to have vigorous birds in the matings.

In 1933 and 1934, the data on feathering were secured when the birds were 8 weeks old. It was decided, however, that 7 weeks was a more critical age and the later data were based on records taken at that age. Therefore, a direct comparison between the results of selection obtained in 1933 and 1934 and those obtained in 1935 and 1936 is not possible.

The results obtained in 1933 showed that selection was of slight effect in bringing about a marked difference in the two strains. During this year four matings were made, two of which were well-feathered while the other two were poor-feathered. The mean feathering scores of the offspring secured from the well-feathered matings were 12.8 and 11.8 for the males and 20.5 and 17.4 for the females, as compared with 11.7 and 12.3 for the males and 17.4 and 16.6 for the females of the two poor-feathered matings. The slight difference between the mean scores of the two selected lines is probably due to the fact that selection in 1933 was accomplished by choosing from mass populations birds showing either extremely good or poor feathering. For the 3 years which followed, selection was carried out on the basis of both individual feathering score and progeny performance. The scores made in 1933 are not strictly comparable to those made in 1934, since the junior author did the scoring the first year. In the succeeding years all scoring was done by the senior author and every effort was made to keep the standards uniform.

A summary of the results obtained in 1934, 1935, and 1936 is presented in table 9. It will be noted that the score of feathering made at 8 weeks of age is considerably higher than that at 7 weeks of age. In 1934, when feathering was evaluated at the age of 8 weeks, 2 well-feathered matings produced 342 birds and 3 poor-feathered matings produced 259 birds which had considerably lower mean scores. Although these values cannot be compared with those of 1935 and 1936 because of the age factor previously mentioned, nevertheless selection during 1934 must have accomplished something in segregating lines differing in their genetic make-up. The difference in score of the two strains is statistically significant.

TABLE 9.—*Results of selection within the well- and poor-feathered strains of Rhode Island Reds for a period of 3 years*

WELL-FEATHERED STRAIN

Year	Males			Females		
	Birds	Mean feathering score	Mean weight	Birds	Mean feathering score	Mean weight
	Number		*Grams*	*Number*		*Grams*
1934 [1]	169	25.4±0.18	521.7± 5.98	173	28.9±0.10	475.6± 5.15
1935	77	9.2± .25	312.5±16.61	54	16.0± .44	306.3±20.67
1936	50	9.0± .31	337.0± 8.18	112	14.0± .24	325.2± 4.26

POOR-FEATHERED STRAIN

1934 [1]	135	20.6±0.27	509.7± 4.83	124	25.4±0.24	466.9± 4.96
1935	59	5.1± .18	330.0± 6.63	36	8.4± .40	316.9± 7.65
1936	58	4.4± .21	325.2± 8.01	75	6.8± .25	300.3± 5.84

[1] In 1934 scoring was done at 8-weeks of age while in later years these records were taken at 7 weeks.

The results for the year 1936 show that selection to obtain better feathering in the well-feathered strain did not effect any improvement over 1935 in either sex, as judged by the mean feathering scores of the years concerned. In 1935 and 1936, three well-feathered matings were made each year. The individual mean feathering scores of the three matings made in 1935 were 8.7, 9.0, and 9.5 points for the males and 23.4, 14.3, and 16.1 points for the females, respectively, while the means for the three 1936 matings of this strain were 9.1, 9.0, and 8.8 points for the males and 13.4, 14.5, and 14.2 points for the females, respectively.

With respect to the influence of selection in the poor-feathered strain, the results presented in table 9 show that the mean feathering scores of both sexes were lower in 1936 than they were in 1935, indicating some effects of selection in the last year's matings. The individual mean feathering scores for the three matings of 1935 were 4.8, 6.1, and 4.9 points for the males and 8.0, 11.2, and 7.6 points for the females, respectively, while those of the four matings made in 1936 were 4.8, 2.6, 3.6, and 6.5 points for the males and 5.4, 5.0, 7.6, and 9.4 points for the females, respectively. In each generation of selection the differences in feathering score of the well- and poor-feathered strains are very definite and statistically significant, indicating that selection had segregated two strains which differed genetically. Representative groups (1936 hatch) of the well-feathered and poor-feathered males at 7 weeks of age are shown in figure 4, *A* and *B*, respectively. Representative females from the well- and the poor-feathered strains at the same age are shown in figure 5, *A* and *B*.

Selection as practiced in these studies necessitated a considerable amount of inbreeding in each of the strains. Despite the fact that mating of closely related individuals was avoided, there appeared during the breeding season of 1935 definite signs of reduced viability among the progeny of the selected lines. There was no significant decline in size of the birds in the selection strains in 1936 over 1935 and it seems that inbreeding was not responsible for the lowered feathering score in the poor-feathered strain.

It is to be concluded that selection for a period of 4 years was effective in segregating strains which differed in their genetic constitution for rate of feathering and that most of the results were accomplished in the first 2 or 3 years of selection.

MATINGS OF THE WELL- AND POOR-FEATHERED STRAINS

F_1 Generation Results

During the 1935 breeding season, reciprocal crosses involving well- and poor-feathered Rhode Island Red strains were made. Each male used was mated to females of his own strain as well as to those from the other strain. This tended to eliminate effects of the individuality of the birds used as parents, making birds of the selection strains for 1935 half brothers and sisters to the hybrids.

A summary of the results obtained from reciprocal crosses between birds of the well- and poor-feathered strains, as well as the selection results for the same year, are given in table 10. In both sexes the mean feathering scores obtained from the reciprocal crosses were virtually

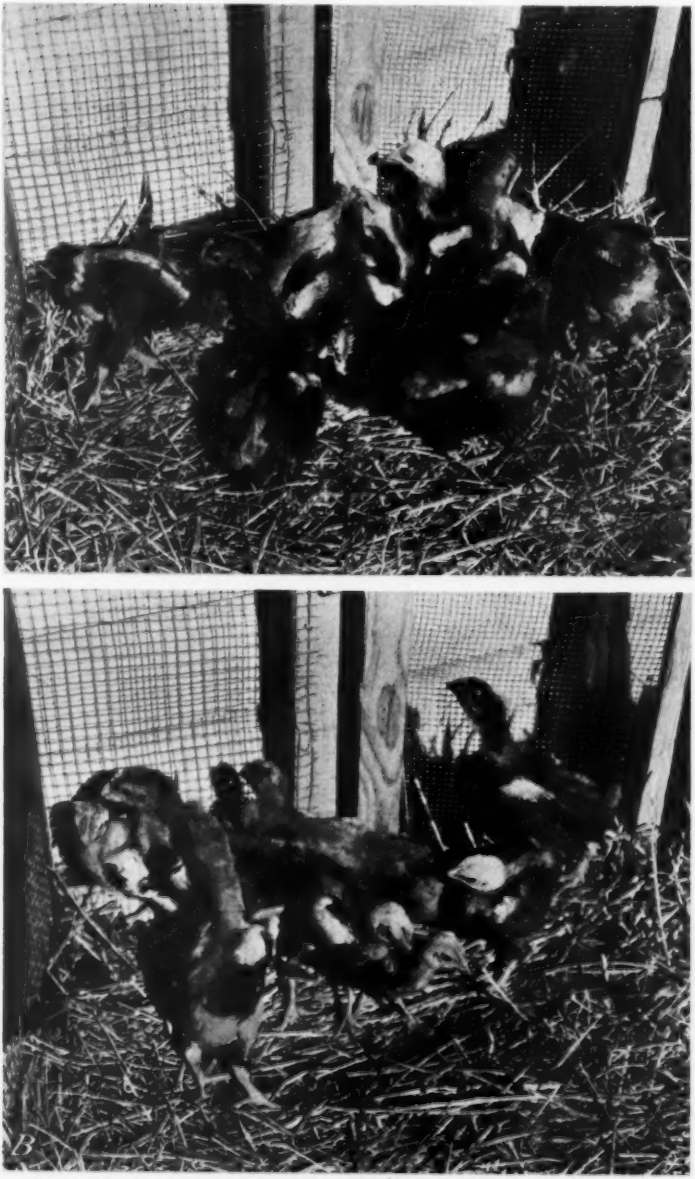

FIGURE 4.—Seven-week-old males from the fourth generation of selections of the well-feathered strain (*A*) and the poor-feathered strain (*B*).

identical, the two groups of hybrid males scoring 8.1 and 8.8 while the females scored 13.8 and 13.1. The distribution of male feathering

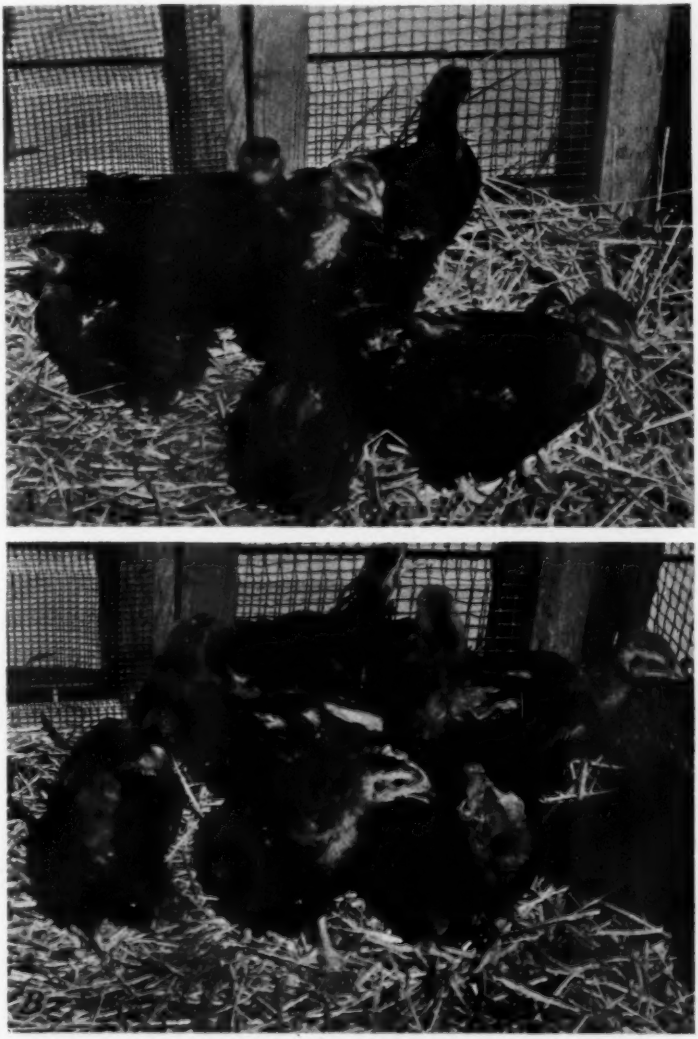

FIGURE 5.—Seven-week-old females from the fourth generation of selections of the well-feathered strain (*A*) and the poor-feathered strain (*B*).

scores made in the F_1 generation, together with those in the two parental strains for the same year, are shown in figure 6.

TABLE 10.—*Effects upon feathering score and body weights of reciprocal matings between well- and late-feathered Rhode Island Reds, 1935*

Mating	Males			Females		
	Birds	Mean feathering score	Mean body weight	Birds	Mean feathering score	Mean body weight
	Number		*Grams*	*Number*		*Grams*
Poor-feathered male and well-feathered female	43	8.1±0.25	345.3±9.31	51	13.8±0.36	338.0±6.17
Well-feathered male and poor-feathered female	61	8.8± .24	371.0± 9.15	53	13.1± .43	333.6± 7.04
Well-feathered strain	77	9.2± .25	312.5±16.61	54	16.0± .44	306.3±20.67
Poor-feathered strain	59	5.1± .18	330.0± 6.63	36	8.4± .40	316.9± 7.65

These results show the condition of well feathering as being incompletely dominant to poor feathering, since the mean feathering

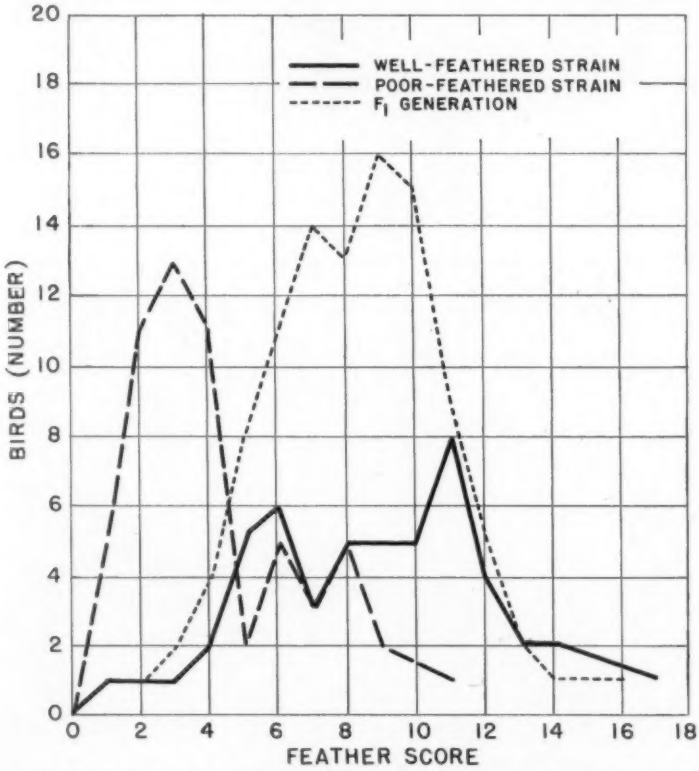

FIGURE 6.—Distribution curves for male feathering scores made in the well- and poor-feathered strains, together with that of the F_1 generation.

scores of the two sexes in the F_1 generation approximate very closely those of the well-feathered strain for the same year. The similarity in feathering score of the F_1 generation females from reciprocal crosses

shows that no important sex-linked factors are involved. Evidence is also adduced from these results that the progeny of these crosses have benefited by hybridization (*21*), as indicated by their mean body weight in comparison with that of the lines of selection in the same year. The growth of feathers did not seem to have been affected in the same manner. The feathering score of the hybrids was similar but slightly less than that of the well-feathered strain for the same year.

Backcrosses

F_1 generation females were backcrossed to males of both parent stocks. For this work females were chosen the feathering score of which was near the mean of the F_1 population. Approximately equal numbers of pullets from each of the reciprocal matings were placed in each pen. Again, in this generation the males used were mated with both F_1 generation females and those from their own strain, making possible comparisons between related pure strain and backcross progeny.

The results of the two backcross matings are summarized in table 11. The 168 birds produced by the matings headed by the well-feathered males had feathering scores of 8.8 and 13.1 points for the males and females, respectively. These two scores approximate very closely the means secured in the F_1 population and also the mean of the well-feathered selection line of 1936. The mean feathering scores of the progeny from the backcross to the poor-feathered parent were 5.7 and 8.7 points for the males and females, respectively. These scores are intermediate between the scores of the well-feathered and those of the poor-feathered strains, which again fits the theory of the dominant behavior of well feathering. Distribution curves of male feathering scores in the backcrosses to the parental stocks are shown in figure 7.

Table 11.—*Effects upon feathering score and body weights of backcross matings of F_1 generation females to the two parent stocks*

Mating	Males			Females		
	Birds	Mean feathering score	Mean body weight	Birds	Mean feathering score	Mean body weight
	Number		*Grams*	*Number*		*Grams*
Well-feathered male and F_1 females	45	8.8±0.27	340.7±4.78	124	13.1±0.25	327.6±4.76
Poor-feathered male and F_1 females	123	5.7± .15	355.6±5.60	150	8.7± .18	324.4±4.28
Well-feathered strain	50	9.0± .31	337.0±8.18	112	14.0± .24	325.2±4.26
Poor-feathered strain	58	4.4± .21	325.2±8.01	75	6.8± .25	300.3±5.84

The results obtained from these backcross matings seem to offer additional support to the view that the condition of being well-feathered is incompletely dominant to poor feathering. This is in agreement with the findings of Jaap and Morris (*9*). In dealing with a quantitative character of this type, it is difficult to determine exactly how many factors are involved, but the genetic behavior of the character is such as to suggest the action of relatively few major factors and that these are autosomal in location. The early establishment by selection of the differences secured would support the view of only a few factors being involved.

RHODE ISLAND RED—WHITE LEGHORN CROSSES

Reciprocal crosses between poor-feathering Rhode Island reds and late-feathering White Leghorns were made to determine the extent to which poor feathering, as it exists in the Rhode Island Reds, differed from late feathering as it is carried by the Leghorns. As stated

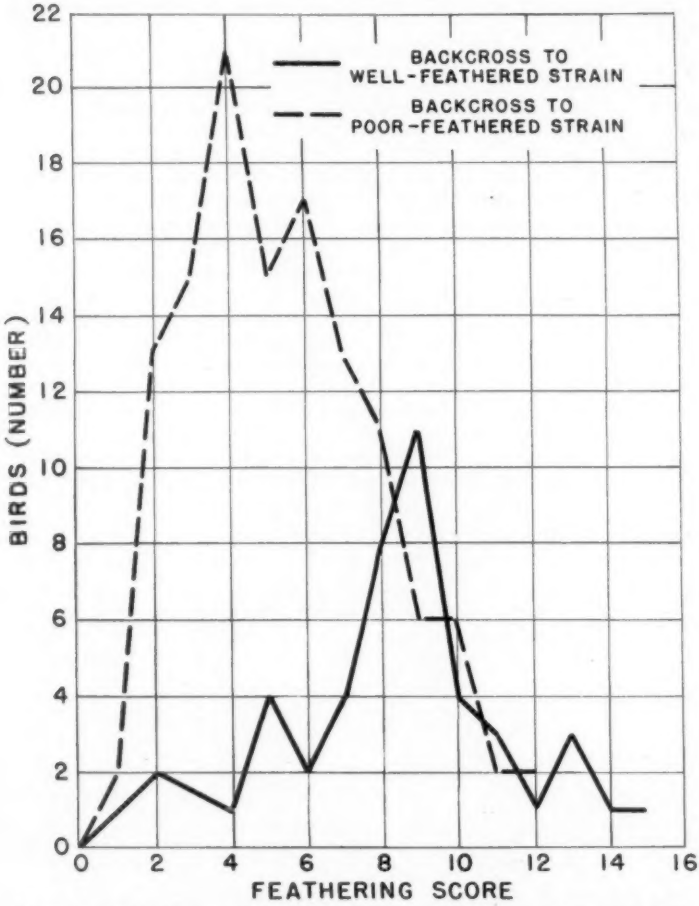

FIGURE 7.—Distribution curves for the male feathering scores in backcrosses to the parental stocks.

previously, the late-feathered Leghorn birds used were the result of selections from a cross of normal-feathered Leghorns and Barred Plymouth Rocks. The ultimate results of these selections were birds very similar to normal Leghorns except that they carried the sex-linked dominant gene for late feathering from the Barred Plymouth Rocks. A total of 129 birds was produced from the mating of the poor-feathered Rhode Island Red cock with late-feathering Leghorn

females. Of these offspring 79 were male and 50 female. The mean feathering score of the males was 8.6 points, while that of the females was 14.1. The reciprocal mating headed by the late-feathered Leghorn male produced 127 birds having a mean feathering score of 8.7 for males and 14.5 for females. The offspring of the reciprocal crosses had almost identical mean feathering scores, and these scores were very similar to those of the well-feathered Rhode Island Red and the F_1 generation of the cross of poor- by well-feathered Rhode Island Reds. Thus in crosses the slow-feathering Leghorn strain behaves genetically very similarly to the well-feathered Rhode Island Red strain. An examination of table 1 reveals the fact that these two strains differ somewhat in the time of feathering, the slow-feathering Leghorns growing feathers somewhat earlier. These differences would suggest that the slow-feathering Leghorns and well-feathered Rhode Island Reds differ genetically to a degree, but these differences are not expressed when the two strains are crossed to the poor-feathered Rhode Island Red strain.

It should be kept in mind that the variations considered in the genetic studies, were those occurring in the strains of Rhode Island Reds known to be homozygous for the dominant sex-linked late-feathering factor. Most strains of Rhode Island Reds carry the late-feathering factor as contrasted with the early-feathering found in Leghorns.

CONCLUSIONS

Well-feathering is incompletely dominant to poor-feathering and is conditioned by autosomal factors. In the case of the sex-linked pairs of genes influencing feathering, better feathering is the recessive. Although physiological relationship between these types of feathering seems evident, their hereditary behavior appears to be quite dissimilar.

DISCUSSION

It appears that the genetic method may offer a simpler approach to the problem of broiler feathering than the physiological one. Nutritional or other physiological methods offer some possibility of improvement of feathering, but they are not always practical or economical. Selection in ordinary late-feathering strains will accomplish rather promptly some improvement in feathering at the broiler stage. The results indicate, however, that a condition of feathering, such as is found in the sex-linked, early-feathering strain, cannot readily be attained by selection of the genetically late-feathering stock. Sex-linked, early feathering, commonly present in the breeds of the Mediterranean class, and occasionally found in individuals of the large breeds, probably offers the most practical solution of the problem. The detection and propagation of the sex-linked early feathering gene in breeds utilized for broiler production is probably the simplest solution for the problem of broiler feathering.

SUMMARY

Vitamin A and the choice of grains used in the ration were of questionable significance in broiler feathering.

Thyroxine injections definitely stimulated feather development.

Brooding chicks under either high humidity or low temperature improved the feathering.

Molt was not a factor influencing the results of the experiments reported.

Selection carried out for a period of 4 years was effective in establishing strains differing genetically in degree of feathering at 7 weeks of age. Most of the established differences were accomplished in the first 2 years of selection.

Better feathering as established by selection was incompletely dominant to poorer feathering. The number of genes involved was not determined but the results would indicate that they are relatively few.

The genetic differences established by selection for degree of broiler feathering were probably due to modifying factors acting upon the sex-linked dominant late-feathering factor.

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SORGHUM CHARACTERS GROUPED BY MULTIPLE CORRELATIONS[1]

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INTRODUCTION

The heritable characters of grain sorghums (*Sorghum vulgare* Pers.), which have been suggested as sources of linkage groups, were used for determining their practical value as a means of indicating yields. The approach has been from a multiple correlation basis. Thirteen such characters have been correlated with yield at various times during eight seasons. Ayyangar and others [2] who conducted a similar investigation over a much shorter period, have drawn the following conclusion: "The total grain yield of a plant can be predicted very closely, when the diameter of the peduncle, length and thickness of the ear head, and the weight of 100 grains are all known."

MATERIAL AND METHODS

A white-seeded grain sorghum, Blackhull, was crossed with an amber-seeded sorgo (sweet sorghum), Japonica, and the hybrid was used throughout the investigation. Blackhull is about two-thirds as high as Japonica; it is nonsaccharine, while Japonica is sweet; its heads are compact, while those of Japonica are loosely branched; and its leaf surface is much smaller than that of Japonica. Head-to-row plantings were made each year, and 10 plants were measured from each of 20 rows. Heads representing a medium between the contrasting characters were selected each year from the rows, thus maintaining a type similar to the F_1 of the original cross.

The 13 characters measured are listed below, together with the method of determining each. Nine independent variables were used each year to check against the yield of grain as the dependent variable. Those found to be of low scoring value were dropped and replaced by more promising ones.

(1) Lengths of seed branches—measured in tenths of an inch by means of a caliper.
(2) Length of plants—measured by a surveyor's rod in feet and tenths of a foot.
(3) Length of heads—measured upon the same rod in tenths of a foot.
(4) Circumference of heads—determined by calipering the greatest diameter.
(5) Length of tip branches—determined by a caliper in tenths of an inch.
(6) Circumference of stalks—estimated from the calipered diameter.
(7) Number of nodes in heads—counted only on plants that developed definite heads.
(8) Number of side branches—counted only on plants that developed definite heads.
(9) Length of the last internodes—measured in feet and tenths of a foot on the surveyor's rod as head and length of plant were determined.
(10) Number of leaves—counted.
(11) Leaf area—determined by means of a planimeter.

[1] Received for publication November 20, 1937; issued May 1938.

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(12) Chlorophyll—determined by a photoelectric colorimeter reading of an alcoholic extract of ground leaf material. These readings are indicated in foot-candles of light passing through a measured amount of solution.

(13) Sugar content—measured in a few drops of freshly expressed juice by a Zeiss hand sugar refractometer. The value for sugar content is expressed as a percentage of the total solids present in the juice. Collections were made each Monday at 9 a. m., and the juice was expressed into the refractometer at once to prevent any decomposition of the sugar. This process was started as soon as the stalks began to show nodes and was continued until the end of the growing season. The percentages are averages of the entire series.

Nine variables were measured for each plant, 10 plants being used from each head-to-row planting. In the case of sugar and chlorophyll determinations, samples were taken each week during the entire growing season and the average was used in the correlations.

The tabulations were made according to the plan of Wallace and Snedecor [3], without classifying into groups. The steps were followed as suggested in their formulae for determining multiple correlation coefficients. Solutions of the beta values are expressed in a multiple correlation coefficient, with a standard error of estimate, for the years 1929–36, as shown in table 1.

TABLE 1.—*Coefficients of multiple correlation and standard errors of estimate, 1929–36*

Item	1929	1930	1931	1932	1933	1934	1935	1936
Coefficients.....percent..	74.2	89.0	76.2	96.2	8.3	77.4	39.5	58.7
Standard error of estimate.....	41.6	64.8	24.6	29.0	2.3	48.7	8.4	30.9

EXPERIMENTAL DATA

In the first 4 years the correlation percentages increased in a significant trend, while the standard error of estimate decreased, but during the last 4 years the results were irregular, with a notable decrease in 1933. Standard errors of estimate imply an unusual variation in the applicability of the data. In 1934, the error was very high as compared to the coefficient of that year, but it was not so divergent as that of 1930. Since it has been suggested that the moisture supply was responsible for these wide variations, the rainfall for the growing periods of the years involved is shown in table 2.

TABLE 2.—*Summer rainfall at the Oklahoma Agricultural Experiment Station, 1929–36*

Year	May	June	July	August	September	October	Total	Average
	Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
1929	8.29	2.11	2.66	.43	2.66	4.38	20.53	3.42
1930	6.23	2.36	.04	3.84	.91	2.02	15.40	2.57
1931	2.02	2.24	3.56	3.67	2.01	.99	14.49	2.41
1932	2.28	6.47	9.56	5.55	.94	3.71	28.51	4.75
1933	1.73	.00	6.81	4.99	1.44	4.15	19.12	3.18
1934	2.68	2.07	.72	3.19	8.95	2.23	19.84	3.30
1935	3.59	10.31	.51	3.08	2.26	2.18	21.93	3.65
1936	4.84	1.91	.37	.00	5.77	2.31	15.20	2.53

Rainfall during the early growing season of 1933 was very light, with a heavy July and August moisture supply. The result was an unusual secondary growth of side branches and small heads during

[3] WALLACE, H. A., and SNEDECOR, G. W., CORRELATION AND MACHINE CALCULATION. Iowa State Col. Pub. 30, 71 pp., illus. 1931.

the latter part of the season. Since Japonica has a tendency to branch more than Blackhull under moist conditions, there are some marked inconsistencies in yield. During 1935 and 1936, the secondary growth occurred later and did not affect the yield as much as it had in 1933. The results in table 3, which shows the comparative scores for each year of the project, may contradict the above supposition. In 1933, the large-scoring factors were length of last node and leaf area, with a small value for number of side branches. Comparative scores are expressed in percentages of the dependent variable.

TABLE 3.—*Comparative scores, showing effect upon yield of each factor*

Factor	1929	1930	1931	1932	1933	1934	1935	1936
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Length of seed branches	41.60	3.0	13.99	6.95	8.0	10.35	1.28	7.57
Length of plant	1.93	15.9	18.05	7.47	6.5	13.42	8.23	0
Length of head	11.93	13.3	16.03	8.79	13.0	(1)	(1)	16.72
Length of tip branch	1.40	15.7	4.06	(1)	(1)	(1)	(1)	(1)
Circumference of head	24.44	26.4	24.52	39.09	.5	16.88	8.92	4.94
Circumference of stalk	0	0	0	(1)	(1)	(1)	(1)	(1)
Number of nodes in head	2.87	7.6	1.05	(1)	(1)	(1)	(1)	(1)
Number of side branches	0	11.7	15.59	1.36	2.0	23.0	7.82	9.37
Length of internode	15.63	6.2	6.41	1.29	37.0	6.67	16.15	11.17
Number of leaves	(1)	(1)	(1)	11.7	(1)	(1)	(1)	(1)
Leaf area	(1)	(1)	(1)	.40	22.0	14.60	37.54	12.54
Chlorophyll content	(1)	(1)	(1)	22.94	11.0	15.99	10.81	18.11
Sugar content	(1)	(1)	(1)	(1)	(1)	(1)	9.25	19.55
Total effect on yield	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.00

[1] Not determined during that year.

Since a large number of variables involves much greater complications and increases the probability of error, those of least significance were dropped. The scores of the last 3 years show that leaf area, chlorophyll, and sugar content formed a large portion of the contributions to yield. The first three lengths measured from a group of comparable value, which Karper and Quinby[4] consider as coming from closely related genes. Leaf area, sugar content, and chlorophyll form a second comparable group, and number of leaves and nodes a third.

TABLE 4.—*Solution of normal equations; simple correlation coefficients, 1935–36*

Variables	Correlation coefficients [1] in class—									
	1	2	3	4	5	6	7	8	9	10
1. Length of seed branches	1.000	+0.432	+0.401	−0.168	−0.242	+0.933	−0.189	−0.019	+0.884	+0.051
	1.000	−.048	+.083	−.138	−.549	+.218	+.056	+.441	−.098	+.468
2. Length of plant	------	1.000	+.161	−.071	−.236	+.079	+.316	+.277	+.217	−.179
	------	1.000	+.149	+.188	+.208	+.155	+.181	−.275	+.419	−.186
3. Leaf area	------	------	1.000	−.181	−.203	+.384	−.084	−.059	+.285	+.385
	------	------	1.000	−.161	−.004	+.233	−.657	−.675	+.082	−.249
4. Chlorophyll content	------	------	------	1.000	+.330	−.028	+.437	+.030	−.134	−.163
	------	------	------	1.000	−.510	+.379	−.067	+.171	+.039	+.008
5. Sugar content	------	------	------	------	1.000	−.201	+.558	+.154	−.216	−.099
	------	------	------	------	1.000	−.207	−.218	−.378	−.195	−.296
6. Circumference of head	------	------	------	------	------	1.000	−.252	+.089	+.779	+.043
	------	------	------	------	------	1.000	−.218	−.029	−.025	−.296
7. Length of last node	------	------	------	------	------	------	1.000	+.142	−.185	−.279
	------	------	------	------	------	------	1.000	−.221	+.705	+.300
8. Number of side branches	------	------	------	------	------	------	------	1.000	−.276	−.077
	------	------	------	------	------	------	------	1.000	−.474	+.165
9. Length of head	------	------	------	------	------	------	------	------	1.000	−.083
	------	------	------	------	------	------	------	------	1.000	+.224
10. Yield	------	------	------	------	------	------	------	------	------	1.000
	------	------	------	------	------	------	------	------	------	1.000

[1] Second line of data shows in each case the 1936 correlation coefficients for comparison with 1935, given first.

[4] KARPER, ROBERT EARL, and QUINBY, J. R. HYBRID VIGOR IN SORGHUM. Jour. Heredity 28: 83–91, illus. 1937.

Table 4 shows that the comparative value of individual determinations for the respective years is slight.

A comparison of sugar content (5) with circumference of head (6) for 2 years shows a negative correlation for both years. In 1935, the same sugar content had a positive correlation with length of last node of 0.588, indicating some significance, but in 1936 it had a negative correlation of 0.218. The negative correlation of sugar content with yield of grain is to be expected, because the so-called high-yielding grain sorghums are seldom sweet-stalked. Leaf area (3) shows a positive correlation of 0.385 with yield in 1935, but in 1936 there was an insignificant negative correlation of 0.249.

TABLE 5.—*Solution of beta values for various factors, 1935–36*

Year	Length of seed branches	Length of plant	Leaf area	Chlorophyll content	Sugar content	Circumference of head	Length of last node	Number of side branches	Length of head
1935	−0.8111	−0.0004	+0.4578	−0.0950	−0.0625	+0.0992	−0.1714	+0.0307	+0.5926
1936	−.1294	−.5637	+.1555	+.4771	−.5574	−.2806	+.0772	−.0268	+.3950

A comparison of values in table 5 confirms the inconsistencies of the correlations shown in table 4. The last pair of values for head lengths may suggest a trend of some significance, but the others have such a wide spread from positive to negative that comment is not necessary. Because of the limited number of samples, there may be some doubt as to the applicability of these measurable characters as indicators of yield.

SUMMARY

Whether yields can be accurately predicted from the several score values indicated in these studies is doubtful, especially in seasons of subnormal rainfall.

The irregular results obtained in 4 of the 8 years show that moisture and temperature have much to do with the correlation values.

A basis for inheritance studies may be found in three groups of values shown in this paper: (1) length of plant and plant parts (head and seed branches); (2) photosynthetic agencies, such as leaf area, chlorophyll, and sugar content, and (3) number of leaves and nodes.

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